THE FORMOSAN SUBTERRANEAN TERMITE (ISOPTERA: RHINOTERMITIDAE) IN LOUISIANA: DISTRIBUTION, COLONY CHARACTERISTICS AND INTERACTIONS, AND CONTROL

By

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To Granddad

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Abstract of Dissertation Presented to the Graduate School
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THE FORMOSAN SUBTERRANEAN TERMITE (ISOPTERA: RHINOTERMITIDAE) IN LOUISIANA: DISTRIBUTION, COLONY CHARACTERISTICS AND INTERACTIONS, AND CONTROL

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A statewide survey on the current distribution of the Formosan subterranean termite (FST), Coptotermes formosanus Shiraki, and other termite species was conducted from January 1999 to January 2002. A total of 796 samples were used in the survey constituting all eight known termite species from Louisiana. The subterranean termite species identified were Reticulitermes flavipes (Kollar), R. virginicus (Banks), R. hageni Banks, and the FST. The drywood termite species identified were Incisitermes snyderi (Light), I. minor (Hagen), Cryptotermes brevis (Walker), and Kalotermes approximatus (Snyder) (Isoptera: Kalotermitidae).

Mark-recapture studies were conducted in Louis Armstrong Park, New Orleans, Louisiana, to locate and characterize individual colonies of the FST from May 1998 to June 2001. Characteristics of thirteen FST colonies included worker weights (ranging from 2.96 to 4.54 mg), foraging territories (ranging from 83 to 1,634 m^2), wood consumption rates (ranging from 0.6 to 5.1 g/monitoring station/day), and foraging population estimates (ranging from 194,132 to 4,487,699). A total of 251 out of 785 trees in the park had active FST infestations. An additional four FST and six R. flavipes colonies were discovered during the study.

Agonistic behavior bioassays were conducted using eleven characterized FST colonies from Armstrong Park. Choice (two-dimensional foraging arenas) and non-choice (petri dish arenas) pairings from each colony revealed a lack of intracolony aggression and a variable amount of intercolony aggression. In choice encounters, there was increased aggression among neighboring colonies and a lack of aggression among distant colonies. These data suggest there are distinct recognition cues, such as a colony odor, involved in intercolony pairings, especially among neighboring colonies in the field.

Beginning in June 2001, three FST colonies were baited using the chitin synthesis inhibitor, hexaflumuron, and eliminated within three months. On two occasions, neighboring colonies reinvaded monitoring stations in the foraging territory of the baited colonies before the total elimination occurred. The third vacated territory was reoccupied six months later by a neighboring FST colony. In all three situations, foraging territories of eliminated colonies were completely reoccupied by neighboring colonies. The release of dyed termites from neighboring colonies confirmed the origins of the invaders.

CHAPTER 1
INTRODUCTION

In recent years, subterranean termite research in the U.S. has focused around the distribution, behavior, and control of the exotic Formosan subterranean termite, Coptotermes formosanus Shiraki (Isoptera: Rhinotermitidae). Beginning in 1998, the U.S. Department of Agriculture, led by the Agricultural Research Service, initiated Operation Full Stop, the National Formosan Subterranean Termite Program. This federally funded program is currently evaluating area-wide control measures for C. formosanus in heavily infested areas of the southeastern U.S. The ability of C. formosanus to establish populations in new areas of the U.S. after human-aided spread has also led to concern on the current distribution and prevention of new introductions. Since the introductions of C. formosanus to Hawaii in the early 1900s (Su and Tamashiro 1987) and the continental U.S. in the late 1950s (Chambers et al. 1988), the current distribution within the U.S. is of great importance, especially after Su and Scheffrahn (1990) listed C. formosanus as one of the five most economically important termite species in the U.S. Recent studies have shown an increase in the current distribution based on actual samples and reports from local agencies throughout the U.S. (Woodson et al. 2001). Human-aided spread was responsible for the introduction of C. formosanus to these new areas (Woodson et al. 2001). At the same time, commonly used liquid termiticides were not able to eliminate entire populations and reduce overall pressure once C. formosanus populations established in these new areas (Su 2003a).

Therefore, it is necessary to conduct further fundamental research on established C. formosanus populations in these areas when evaluating control measures. Many researchers have used mark-recapture experiments with oil-soluble dyes, such as Sudan Red 7B, to better understand subterranean termite populations, such as C. formosanus, in urban settings (Lai et al. 1983, Su et al. 1984, Su and Scheffrahn 1988b, Grace and Abdallay 1990). These dyes will remain visible in the termite body for several months after termites are fed dyed filter paper. Dyes, such as Nile Blue A, are relatively safe at proper doses to handle and will not affect the health or behavior of marked and unmarked termites. The foraging population of an urban termite colony can be effectively estimated using a weighted mean model (Begon 1979), in addition to delineating the foraging territory, by incorporating these dyes into a multi-release study, such as triple mark-recapture studies (Su and Scheffrahn 1988b, Su et al. 1993).

In Louisiana, relatively few mark-recapture studies have been conducted on C. formosanus and other native subterranean termite species. Established C. formosanus activity was first discovered in Lake Charles and New Orleans by the mid-1960s (Spink 1967). Beginning in 1966, some of the first biological studies on C. formosanus colonies established in the continental U.S. were conducted in the swampy areas of Lake Charles (King and Spink 1969, 1974, 1975). One of these studies involved the first and only exhaustive field study to delineate the foraging territory by excavating entire foraging gallery systems of C. formosanus colonies infesting trees along the Calcasieu River (King and Spink 1969). Other characteristics of a C. formosanus colony were not established during this study; however, a significant amount of information was determined on the foraging behavior of C. formosanus. Since then, further studies on C. formosanus colonies along the Calcasieu River in Lake Charles have evaluated mean worker weights (Waller and La Fage 1988), wood consumption rates (Delaplane et al. 1991), population estimates (Su and La Fage 1999), seasonal foraging patterns (Waller and La Fage 1987), and control techniques (Henderson and Forschler 1996).

Only a limited amount of mark-recapture research has been conducted on urban populations of C. formosanus in New Orleans. In 1996, triple mark-recapture studies were conducted on the historical Creole House of the Cabildo Complex in the French Quarter (Su et al. 2000). Data from a single C. formosanus colony revealed a population size estimate of approximately 777,000 with a wood consumption rate of 13 g of wood/station/day and a mean worker weight of about 3.5 mg. The foraging territory of the C. formosanus colony on the ground floor was connected with activity on the second floor after the release of dyed individuals and comparing mean worker weight values. After characterization, further studies involved elimination using baits containing an insect growth regulator, monitoring dispersal flight activity, and continued monitoring in the structure for possible reinvasion from termite colonies in the neighboring structures and area.

Beginning in 1998, I began working on a similar project in Louis Armstrong Park, but on a much larger scale than previous French Quarter studies. Louis Armstrong Park is a 12.75 ha public park located near the French Quarter in New Orleans that has had a long history of C. formosanus activity and lack of treatment. Consequently, this City-owned park was an ideal site to better understand C. formosanus colony dynamics, control, and succession ecology, as part of the area-wide termite reduction program in New Orleans. One of the main goals of the Operation Full Stop program is to reduce termite populations within a 15-block area of the French Quarter. However, since this program relies solely on the application of traditional liquid termiticidal and baiting treatments, the overall number of termite colonies, their interactions, and the impact of creating termite-free areas subject to reinvasion were not taken into consideration. The use of baits containing the insect growth regulator, hexaflumuron, has demonstrated in the past significant reductions in termite populations from a given structure and/or area (Su 2003b). If an area-wide termite control project in a heavily infested area is to be successful, then continued monitoring and baiting will be required to eliminate existing and future populations (Su 2003b).

Therefore, the main objectives of this study were to 1) conduct a survey to determine the current distribution of C. formosanus and other termite species in Louisiana, 2) conduct mark-recapture studies to characterize field colonies of the C. formosanus in Louis Armstrong Park, 3) conduct laboratory bioassays on aggressive behavior among these colonies, and 4) selectively eliminate three colonies using baits containing hexaflumuron and monitor for reinvasion by neighboring colonies.

CHAPTER 2

CURRENT DISTRIBUTION OF THE FORMOSAN SUBTERRANEAN TERMITE AND OTHER TERMITE SPECIES (ISOPTERA: RHINOTERMITIDAE, KALOTERMITIDAE) IN LOUISIANA[1]

Introduction

The Formosan subterranean termite, Coptotermes formosanus, was first identified in Lake Charles, Louisiana, in 1966 and in New Orleans in 1967 (Spink 1967). It is widely believed that this non-endemic species was introduced into the continental U.S. after infested material was brought over from Asia after World War II (Su and Tamashiro 1987). For the past 30 years, C. formosanus infestations have been found in other cities and various small communities throughout Louisiana. The main source of introduction to these other areas is caused, in part, by the transportation of infested building materials, utility poles, and railroad ties used in landscaping (La Fage 1987). Then, natural spread has occurred via alate dispersal flights.

The last statewide survey involving the pest control community for all termite species was conducted around the time of the first confirmed report of C. formosanus (Weesner 1965). During the last survey, species and flight data were only recorded from Rapides Parish, which includes the city of Alexandria. Reticulitermes flavipes, R. virginicus (Banks), R. hageni Banks (Isoptera: Rhinotermitidae), and Incisitermes snyderi (Light) (Isoptera: Kalotermitidae) were collected from this region of the state.

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[1] Reprinted by permission from Florida Entomologist. Messenger, M.T., N.-Y. Su, and R.H. Scheffrahn. 2002. Current distribution of the Formosan subterranean termite and other termite species (Isoptera: Rhinotermitidae, Kalotermitidae) in Louisiana. Fla. Entomol. 85: 580-587.

Previously, Light (1934) and Snyder (1954) listed five species in Louisiana. They included R. flavipes, R. virginicus, Kalotermes (=Incisitermes) snyderi, Kalotermes approximatus (Snyder), and Cryptotermes brevis (Walker) (Isoptera: Kalotermitidae). Recently, Messenger et al. (2000) discovered established populations of Incisitermes minor (Hagen) (Isoptera: Kalotermitidae) in New Orleans.

Since the last national survey in 1965, individual statewide termite surveys have been conducted in Georgia (Scheffrahn et al. 2001), Florida (Scheffrahn et al. 1988), Texas (Howell et al. 1987), and South Carolina (Hathorne et al. 2000). These surveys significantly contributed to our understanding of the current distribution of the economically important FST.

Because there have been many unconfirmed reports of C. formosanus throughout the state, the main objective of this survey was to identify and confirm the current distribution of the C. formosanus in Louisiana with the help of the pest control industry, the Louisiana Department of Agriculture and Forestry, and mosquito control districts. In addition, I, with support from the New Orleans Mosquito and Termite Control Board, concurrently conducted a separate statewide survey for all subterranean and drywood termite species.

Materials and Methods

Pest management professional (PMP) survey. Beginning in January 1999, letters asking for participation in the survey were mailed to 589 PMPs and mosquito control districts throughout Louisiana, including a few pest control companies operating near the state line in Mississippi and Texas. Termite collecting packets were then prepared and sent to each company who returned the postcard with a response of willingness to participate. Each packet included individually numbered collection vials (13 ml polypropylene Snap-Seal®, Corning Brand) containing 85% ethanol, corresponding vial data sheets, return padded envelopes, and a hand-held aspirator. Participants were encouraged to collect termite alates and soldiers during routine inspections and treatments of residential and commercial structures. They were also encouraged to include any relevant information from each collection on the data sheet, which included date and location of collection, flight date (if applicable), and any additional comments and requests for more collection vials.

N. O. Mosquito and Termite Control Board (NOMTCB) survey. Along with other coworkers, I conducted a deliberate survey throughout Louisiana from 1999 to 2001. In addition, samples and C. formosanus locations were received from J. McPherson (Program Coordinator, Pesticide and Environmental Programs, Louisiana Department of Agriculture and Forestry, Baton Rouge, LA). Termites were collected from live and dead trees, state parks, railroad ties, highway rest areas, private and public buildings, and any other type of wood found along highways and parish roads. I also traveled to addresses throughout the state to verify C. formosanus infestations and conduct further surveys in the surrounding areas.

For both surveys, termite alates and soldiers were identified to species using termite keys developed by Banks and Snyder (1920), Miller (1949), Snyder (1954), Weesner (1965), Scheffrahn and Su (1994), and Hostettler et al. (1995). Samples containing only workers (Reticulitermes spp.) or pseudergates were identified to the family and/or genus level. Data from both surveys was entered into a computer database (FileMaker® Pro 3.0, Claris® Corporation). Longitude and latitude coordinates from the

NOMTCB survey were recorded at each sample site using a Garmin GPS model 12 CX (Garmin International, Inc., Olathe, KS) hand-held global positioning receiver. Locations of each collection were plotted using ArcView GIS version 3.1 software (Environmental Systems Research Institute, Inc., Redlands, CA).

Results

PMP survey. Out of the original 589 survey letter mailings, 91 (15%) companies and individuals agreed to participate by collecting any type of termite they encountered during routine inspections and treatments of urban structures and trees. There was no response from 453 (77%) companies and 45 (8%) responded, but declined to participate. The majority of the companies who declined indicated that they do not conduct termite treatments.

As a result, 52 of the 91 participants returned collection vials for a total of 426 samples. All eight known termite species were collected (Table 2-1). The majority of these samples were collected from separate addresses. Reticulitermes flavipes was the most commonly collected species throughout the state (Table 2-1). Coptotermes formosanus was the second most commonly collected species; however, the majority of these samples were collected from the New Orleans and Lake Charles areas.

Each participant also included an exact or approximate date of dispersal flight whenever they collected alates. For the subterranean species, R. flavipes alates were recovered from Jan. 17 to April 19, R. virginicus alates from March 1 to May 17, R. hageni on Dec. 17, 2001 (single record), and the FST from April 12 to May 9. For the kalotermitid species, I. snyderi alates were recovered from May 10 to June 18, C. brevis from May 9 to June 9, and K. approximatus from Oct. 10 to Nov. 1. Alate samples of I.

minor were collected from Sept. 10 to Dec. 4 in Rayne, Cameron, and Le Moyeu, LA; however, monitoring of dispersal flights in the New Orleans metropolitan area occurred each year from late April to early June.

NOMTCB survey. Reticulitermes flavipes was by far the most commonly collected termite species throughout Louisiana (Table 2-2). Reticulitermes hageni and R. virginicus were the two second most commonly collected species (Table 2-2). The number of C. formosanus collections represents only a few selected, confirmed sites throughout the state and does not include any samples taken from New Orleans. The distribution of C. formosanus infestations in Louisiana has significantly increased since 1966 (Table 2-3).

In New Orleans, C. formosanus flight activity was monitored using glue traps (TRAPPER® LTD, Bell Laboratories, Inc., Madison, WI) installed under lights near the French Quarter. Nightly observations and the number of alates recovered from glue traps reveal peak flight activity usually occurs from mid-May to early June, with some activity through mid-July (Table 2-4).

The majority of the I. minor and C. brevis samples were received from J. McPherson and local residents of New Orleans.

Location data from both surveys for C. formosanus (Fig. 2-1), Reticulitermes species (Fig. 2-2), and kalotermitid species (Fig. 2-3) are presented on ArcView-generated maps.

Discussion

The distribution of C. formosanus in Louisiana has increased dramatically since the first confirmed reports in the mid-60s. However, many of these newer, confirmed infestations have remained relatively localized, and state officials have begun to target these areas for immediate treatment. Most of these localized introductions have occurred around structures, such as churches, or parks and campsites where infested railroad ties were used as landscaping and/or building material. Future monitoring and confirmation of any new C. formosanus reports throughout the state are the first steps to controlling human-aided spread.

Outside the New Orleans and Lake Charles areas, R. flavipes and R. virginicus are the two most economically important subterranean termite species, with R. flavipes being the most common. The spatial distribution of all three Reticulitermes species is consistent statewide; however, R. flavipes seems to be more common in the extreme southern portions of the state. For example, samples of R. flavipes were collected from house pilings directly in the sand at Holly Beach on the Gulf of Mexico and from fishing camps around the Mississippi River delta basin.

During the PMP survey, R. hageni was rarely encountered in structures. In addition, K. approximatus was only collected from dead portions of trees and from alates flying into the vehicles of participants on two separate occasions. For both species, this confirms their general status as very limited structural pests (Weesner 1970, Scheffrahn et al. 1988).

Incisitermes snyderi and C. brevis are the two most economically important kalotermid species in Louisiana, with I. snyderi being the most common. Cryptotermes brevis is a non-endemic species and has only been recovered from structural lumber and furniture. Incisitermes snyderi is an endemic species commonly found in structural lumber and in dead portions of live trees throughout the southern half of the state.

The overall number of I. minor collections throughout the state was unexpectedly high. Another interesting discovery was the number of public schools throughout the state with very active I. minor infestations, particularly in window framework. Incisitermes minor is endemic to CA, AZ, and Mexico, but has been introduced to many areas in the state, and in most cases, inside furniture. For example, a sample was taken from an infested pool table in Natchez, MS. In New Orleans, I. minor alates are usually collected from mid-April to mid-June during midday flights. However, alates were recovered after swarming from a window frame in an elementary school in Rayne, LA, during the second week of September 2001. In addition, I. minor alates were collected after swarming in a high school in Cameron, LA, in late September 2001. Historical records reveal the flight season of I. minor usually occurs from July to December, and as early as May in the laboratory (Harvey 1934). In addition, I. minor flight records in California (Snyder 1954), Florida (Scheffrahn et al. 1988), and Georgia (Scheffrahn et al. 2001) revealed swarming usually occurs from September to November. An alarming discovery revealed I. minor alates swarming in a lumberyard near Le Moyeu, LA, in December 2001. This could lead to future introductions throughout the state.

In addition to the overall survey, a pictorial termite identification key was developed in 2001 to help PMPs, state officials, and termite researchers identify C. formosanus and other economically important subterranean and drywood termite species currently present in Louisiana (Messenger 2002).

Table 2-1. Total number of identified termite species from vials collected during the PMP survey.

Termite Species	Number of vials
Reticulitermes flavipes	204
Coptotermes formosanus	118
Reticulitermes virginicus	40
Incisitermes snyderi	9
Cryptotermes brevis	7
Incisitermes minor	3
Kalotermes approximatus	3
Reticulitermes hageni	3
workers/pseudergates only	39
TOTAL	426

Table 2-2. Total number of samples, listed by termite species, collected during the NOMTCB survey.

Termite Species	Number of Collections
Reticulitermes flavipes	177
Reticulitermes hageni	65
Reticulitermes virginicus	64
Coptotermes formosanus	36
Incisitermes snyderi	14
Incisitermes minor	8
Cryptotermes brevis	5
Kalotermes approximatus	2
TOTAL	371

Table 2-3. Location of C. formosanus infestations in Louisiana, 1966 - 2002.

Year	Parish	City
1966*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles
1968*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles
	Jefferson	Grand Isle
	La Fourche	Raceland
1986*	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles, Westlake
	Jefferson	Metairie, Gretna, Grand Isle
	La Fourche	Raceland
	St. Tammany	Slidell, Covington
	Lafayette	Lafayette
	East Baton Rouge	Baton Rouge
2001	Orleans	New Orleans, Algiers
	Calcasieu	Lake Charles, Westlake, Moss Bluff, Sulphur
	Jefferson	Metairie, Gretna, Grand Isle, Kenner, Harahan, Westwego, Marrero
	La Fourche	Raceland, Thibodaux, Larose, Cut Off, Galliano
	St. Tammany	Slidell, Covington
	Lafayette	Lafayette
	East Baton Rouge	Baton Rouge
	Ascension	Prairieville
	St. Charles	Norco
	Assumption	Pierre Part
	Terrebonne	Houma, Montegut
	St. Bernard	Chalmette
	Plaquemines	Belle Chase
	Iberia	New Iberia
	Vermilion	Abbeville
	St. Landry	Sunset
	Sabine	Noble
	Ouachita	Monroe, West Monroe
2002**	Acadia	Rayne
	St. Mary	Amelia

*La Fage 1987.

**Records from two new parishes in addition to 2001 reports.

Table 2-4. Combined alate flight dates for C. formosanus in New Orleans, Louisiana, from 1998 to 2001.

Date	Year	Date	Year	Date	Year
May 4	1998	2nd week of Jan.	2000	April 8	2001
May 11		2nd week of Feb.		April 13	
May 16		March 26		April 14	
May 18 *		April 18		April 15	
May 19		April 25		April 16	
May 22		April 29		April 24	
May 26		May 3		May 1	
May 29 *		May 4		May 4	
June 6		May 5		May 5	
June 8		May 8		May 7	
June 18		May 10		May 9	
June 21		May 14		May 12	
June 23		May 15 *		May 13	
June 28		May 21		May 14	
2nd week of Feb.	1999	May 22		May 15 *	
April 6		May 26		May 17	
April 26		May 29		May 20	
April 27		June 4		May 21	
April 28		June 15		May 22	
May 6		June 16		May 23	
May 7		June 17		May 24	
May 12 *				May 25	
May 14				May 26	
May 17				May 31	
May 18				June 1 *	
May 19				June 4	
May 25				June 7	
May 27				June 11	
May 29 *				June 14	
June 6				June 18	
June 9				June 21	
June 10				June 24	
June 22				June 28	
June 27					
1st week of July					
July 7					
July 13					
3rd week of July					

* Largest dispersal flight(s) each year

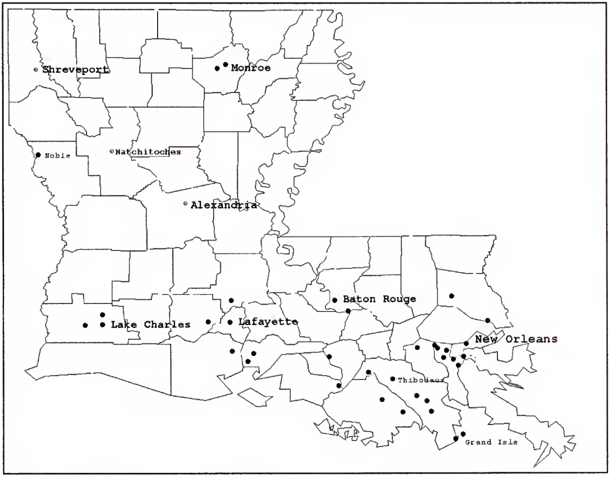

Figure 2-1. Current localities of C. formosanus in Louisiana.

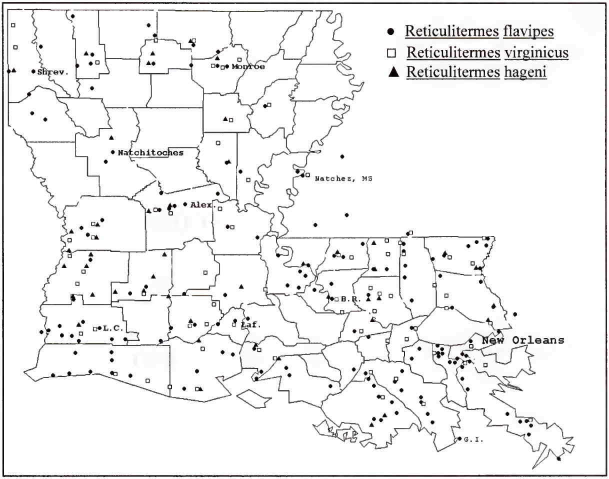

Figure 2-2. Combined locality data of Reticulitermes spp. in Louisiana from PMP and NOMTCB surveys.

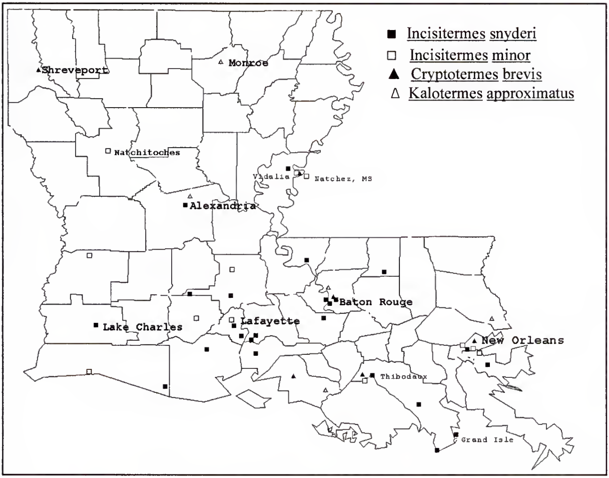

Figure 2-3. Combined locality data of kalotermitid species in Louisiana from PMP and NOMTCB surveys.

CHAPTER 3

COLONY CHARACTERISTICS OF THE FORMOSAN SUBTERRANEAN TERMITE IN LOUIS ARMSTRONG PARK, NEW ORLEANS, LOUISIANA

Introduction

In the past few decades, mark-recapture procedures for characterizing subterranean termite colonies have been used extensively for R. flavipes (Esenther 1980, Grace et al. 1989, Su et al. 1993, Forschler and Townsend 1996), R. hesperus Banks (Haagsma and Rust 1995), Heterotermes aureus (Snyder) (Isoptera: Rhinotermitidae) (Jones 1990), and the Formosan subterranean termite, Coptotermes formosanus (Lai 1977, Su and Scheffrahn 1988b). Important colony characteristics that can be determined using this procedure include mean worker weight, foraging territory area, wood consumption rate, and a foraging population estimate. Probably the single most important result of establishing monitoring stations and releasing dyed termites is delineating the foraging territory of a given colony, especially when a subterranean termite colony is defined as a group of termites sharing interconnecting tunnels (Su 2001, Su and Scheffrahn 1998). Once this type of information has been established for a given colony, then evaluating the effectiveness of a chosen termiticide or baiting system can be determined. Upon treatment, the foraging territory and wood consumption rate for a colony should be affected in a manner that is noticeable in the monitoring stations and consistent with the treatment (Su and Scheffrahn 1996).

Beginning in May 1998, multiple mark-recapture studies were conducted in Louis Armstrong Park, New Orleans, to locate, identify, and characterize every C. formosanus colony before conducting further behavioral bioassays and treatments. Louis Armstrong Park is a fenced-in, 12.75 ha, city-owned urban park located to the northwest of the French Quarter in New Orleans. The four major structures in the park include the Morris FX Jeff Municipal Auditorium, the Mahalia Jackson Theater for the Performing Arts, a City of New Orleans Sewerage and Water Board pumping station, and the Perseverance Hall complex (Fig. 3-1). The park has had a long history of C. formosanus activity dating back to one documented introduction in 1973 of an infested stage that was placed inside the Theater (Scott and Scott 1996). The stage originated from Camp Leroy Johnson, which was one of several military bases credited to introducing C. formosanus from Asia to New Orleans after World War II (La Fage 1987).

Previously, the only documented termite control research in the park occurred in 1996 for Perseverance Hall (the oldest Masonic Temple in the Mississippi Valley) and its associated historical buildings to evaluate the efficacy of the Sentricon® Termite Colony Elimination System (Dow AgroSciences, Indianapolis, IN) (Freytag et al. 2000). After an 11-month baiting period, all C. formosanus activity ceased inside the building and inside the monitoring stations confirming colony elimination. Therefore, the Perseverance Hall complex was the only area within the park that lacked C. formosanus activity at the beginning of this study.

The remainder of the park is comprised of three large parking lots, an artificial concrete lagoon, driveways and walkways, planters, and grass areas with planted trees (Figs. 3-1, 3-2, and 3-3). The test site is completely bounded by city streets. A preliminary, visual survey of the area revealed extensive C. formosanus activity in these trees. Besides Perseverance Hall, every other building is concrete and steel with a limited amount of wood infrastructure, suggesting most of these colonies were feeding strictly on trees within the park. The objectives of this study were to 1) determine how many C. formosanus colonies were present, 2) delineate each foraging territory, 3) determine the foraging activity as expressed by the wood consumption rate of each colony, 4) estimate the foraging population for each colony using a weighted mean model, and 5) monitor dispersal flight activity inside and along the perimeter of the park.

Materials and Methods

Tree survey. In April and May 1998, every tree inside the park, including trees located just on the other side of the perimeter fence, was thoroughly inspected for any evidence of live C. formosanus activity. Then, tree species and location was determined. All trees were periodically inspected from 1998 to August 2001 for termite activity. The Sibtec Scientific Decay Detecting Drill (DDD) (Sibert Technology Ltd., Surrey, England) was used to confirm active trees by locating galleries inside the tree. In addition, holes were drilled in some trees using a gas-powered auger drill with a 9.525 mm drill bit, and soldiers would immediately surface from inside if the tree was active. These holes were then plugged with a wooden dowel for future monitoring purposes.

Mark-recapture studies. In April 1998, over 1,500 pine (Pinus sp., 1.7 x 3.7 x 32.1 cm) stakes were driven into the soil approximately every meter in grass and shade areas, including planters, throughout the park to locate any subterranean termite activity. In addition, stake placement was concentrated along ground level roots of heavily infested trees. These stakes were checked approximately every two to three weeks for the presence of termites. Active stakes were replaced with underground monitoring stations (UMS), as described by Su and Scheffrahn (1986). Each UMS consisted of a

3.78-liter plastic bucket with a removable lid installed approximately 30 cm in the soil with 3 cm cut out from the bottom. Then, pre-weighed wood blocks consisting of either 36 slats (~3.5 by ~13 cm by ~2 mm) or 18 slats (~8 by ~13 cm by ~3 mm) of spruce (Picea sp.) bound together were placed inside each UMS, along with the termites collected from the stake. Every UMS was concealed in the soil to prevent any tampering within the public park. Each UMS was checked about every three to four weeks after installation and the block was replaced if a sufficient number of termites (>200 individuals) were present and/or at least half of the block was consumed. Field collected blocks and termites were returned to the laboratory and processed in less than 24 hrs. Termites were carefully separated from the slats and debris and eventually workers, soldiers, and other castes were separated from each other and kept in temporary containers using the method described by Tamashiro et al. (1973). Sub-samples (5 sets of 20 > 3rd instar workers, 1 set of 20 soldiers) were taken so that individual weights could be calculated for each caste and then the total number collected could be calculated. In some cases, workers and soldiers were individually counted after taking sub-sample estimate weight measurements to confirm accuracy. Then, termites were placed in 100 x 15 mm petri dishes containing filter paper (Whatman No. 1) dyed with either Nile Blue A (0.1% w/w), Neutral Red (0.5% w/w), or Sudan Red 7B (0.5% w/w) (Fisher Scientific, Pittsburgh, PA). Approximately 2 g of termites were placed in each petri dish and remained for at least six days, or until the majority of workers had ingested a visibly sufficient amount of dye. They were then removed from the petri dishes, weighed and counted again, and released back into the UMS they were originally collected from. Marked termites were now present in the field and the colony foraging territory could be slowly defined after observing dyed termites in stakes, trees, and structures near the release site. Additional UMSs were installed when dyed termites were found in stakes near the original UMS release site. In many cases, additional stakes were added next to active stakes instead of UMSs. Wood blocks were collected again after a few weeks (depending on termite activity) from all available UMSs from a particular area. The number of dyed termites recovered from each UMS was recorded and termites were weighed and counted, fed dyed filter paper again, and released back into their respective UMSs. Only termites from UMSs containing dyed termites were dyed and released, especially after the first release had occurred, to avoid errors in differentiating between two colonies possibly present in the same territory. In a few cases, mark-recapture studies were completed with one colony before beginning a study with a neighboring colony. Also, if two colonies were present in a defined area, then one colony was dyed with Nile Blue A and the other was dyed with either Neutral Red or Sudan Red 7B.

Foraging territory. The foraging territory of each C. formosanus colony was determined by connecting monitoring stations, stakes, and trees containing termites dyed with the same markers. Foraging territories were mapped on a geo-referenced, aerial orthophoto image (1 pixel = 0.8 square foot) of Louis Armstrong Park using ArcView GIS version 3.1 software (Environmental Systems Research Institute, Inc., Redlands, CA).

Wood consumption rate. Blocks collected in the field were first separated from the termites and loose debris was removed. The wood consumption rate (pixel loss/UMS/day) was calculated using the technique of Su and Messenger (2000). The wood consumption rate over time was estimated using video image analysis based on the amount of pixel loss (~1,000 pixels = ~0.9 grams of wood) for each block.

Foraging population estimate. Using a weighted mean model (Begon 1979), an estimate and associated standard error of the foraging population was calculated after conducting a triple mark-recapture study (Su et al. 1993) on each colony. Termites from each colony were dyed and released for at least three cycles, usually within three months.

Dispersal flight activity. All subterranean termite dispersal flight activity in the park was monitored from 1999 to 2002 using 68 glue traps (20.7 cm X 10.2 cm, TRAPPER® LTD, Bell Laboratories, Inc., Madison, WI) installed on light posts in one section of the park (34 traps), traps hanging along the perimeter fence surrounding the park (28 traps), and traps hanging from a magnolia tree within the Perseverance Hall Complex (6 traps) (Fig. 3-8). A New Jersey light trap was installed in approximately the center of the park (Fig. 3-8). Traps were installed before the start of the C. formosanus dispersal flight season (Feb. and March from 1999 – 2001, April in 2002) and removed by mid-July. Each trap was checked and replaced weekly and biweekly, and the total number of C. formosanus and other alate species recovered was counted.

DNA fingerprinting. Beginning in mid-2000, samples of workers, soldiers, and alates were collected and saved for future analyses. Approximately every six months, 50-100 individual termites from each UMS, and occasionally from infested stakes and trees, were placed in vials containing 100% ethanol for DNA fingerprinting at the University of Hawaii.

Statistical analysis. The relationship between colony characteristics (mean worker and soldier weights, foraging territory, wood consumption rate) was examined using regression and correlation analyses (SAS Institute 2000).

Results

Tree survey. A comprehensive, visual inspection survey of every tree in the park representing 24 tree species in 17 families revealed approximately 32% showed active C. formosanus infestations and/or damage (Table 3-1). Every infested tree showed some form or another of termite attack, ranging from mud tubes to previously fallen limbs. Except for the Perseverance Hall complex area of the park, the number of infested trees was widely distributed throughout the park (Fig. 3-4). The four most commonly infested tree species included live oak, baldcypress, red maple, and sycamore (Table 3-1). Only six tree species showed no evidence of termite attack (Table 3-2).

Mark-recapture studies. Approximately 100 stakes were active with C. formosanus when all stakes were checked in early May 1998. At the same time, ten stakes were active with R. flavipes. Underground monitoring stations (UMSs) were installed directly on 54 active stakes. Then, triple mark-recapture studies were performed on individual colonies revealing the presence of at least thirteen individual C. formosanus colonies (Fig. 3-5) and six R. flavipes colonies (Fig. 3-7). The foraging territories of each C. formosanus colony never overlapped and were separated by zones of inactivity. Many R. flavipes colonies had foraging territories that overlapped with C. formosanus territories (Fig. 3-7). On two occasions, an UMS located in foraging territories of both C. formosanus colony # 1 and C. formosanus colony # 2 were seasonally shared with each R. flavipes colony, with R. flavipes activity during colder months (Dec. – Feb.) and C.

formosanus activity throughout the remainder of the year. Two C. formosanus colonies present along the border of the park were not characterized, along with two other colonies with small foraging territories that were first discovered in 2000 (Fig. 3-6). These four colonies were never connected to any foraging territories of characterized colonies via marked individuals.

Foraging territories for each characterized C. formosanus colony were located along the perimeter and interior grass areas of the park situated amongst the planted trees, which were located predominantly along the perimeter (Fig. 3-5). Dyed individuals were recovered from inside many trees within each territory confirming a connection with ground UMS activity. Activity from C. formosanus colony # 5 and # 6 was detected under the concrete parking lots approximately two meters from the nearest UMS after a few 76.2 mm cored holes were drilled and fitted with pine stakes in early 2000.

Characteristics determined for each colony included mean worker weight, mean soldier weight, foraging territory area, wood consumption rate, and foraging population estimate (Table 3-3). It became evident after visual observations over time that workers and soldiers within UMSs and throughout the foraging territory of each colony were very similar in size and distinctly different from neighboring colony individual sizes (Table 3-3). As a result, worker and soldier weights showed a significant correlation ($r = 0.8852$, p-value < 0.0001, Fig. 3-12). There was also a significant correlation between worker weights and foraging territory size ($r = 0.3429$, p-value < 0.0001, Fig. 3-13) and worker weights and wood consumption rates ($r = 0.1916$, p-value < 0.0001, Fig. 3-14); however, the correlation coefficient was very low for both comparisons. Wood consumption rate values represent consumption rates throughout each year, which led to the higher variability in each comparison after correlation analysis. There was no significant correlation between foraging territory size and wood consumption rate (Table 3-4). The foraging population numbers were not analyzed statistically with other variables because each number only represented an estimate, and therefore variation could not be accounted for.

Over time, the percentage of active UMSs ranged from 22% to 100% revealing distinct peaks and troughs in activity each year (Fig. 3-9). Wood consumption rate estimates varied from 0.6 to 5.1 g of wood consumed/UMS/day when pixel loss was converted to grams (Table 3-3). The standard deviation was very high for each colony because wood consumption was combined over time. The overall consumption rate revealed distinct peak and troughs in activity each year and from year to year (Fig. 3-10). Plotting combined wood consumption rate data for all C. formosanus colonies with the combined percent of active UMSs revealed a distinct, positive relationship (Fig. 3-11).

Dispersal flight activity. Coptotermes formosanus was by far the most commonly collected termite species during dispersal flight monitoring from 1999 to 2002; however, four other alate species were also recovered each year (Table 3-5). The majority of C. formosanus alates were collected during the second and last weeks of May and during the first week of June (Fig. 3-15). There were also at least one or two major dispersal flights each year based on field observations and overall number collected. The first swarm occurred during May 12 – 18 and the second (if present) occurred during May 29 – June 1 (Chapter 2, Table 2-4).

Reticulitermes flavipes and R. virginicus, were recovered from Jan. to April, with R. flavipes being recovered in Jan. and Feb. and R. virginicus in March and April.

Reticulitermes flavipes was not collected in 2002 because glue traps were installed in early April. Incisitermes minor and I. snyderi were also recovered during peak FST flight activity in May (Table 3-5).

DNA fingerprinting. After completion of mark-recapture studies in the park, results from DNA fingerprinting analysis confirmed the genetic individuality of each C. formosanus colony (Husseneder et al. 2003). Pools of individuals from each UMS in each territory were used to provide colony profiles with diagnostic bands unique to each colony, thus supporting mark-recapture studies in identifying separate C. formosanus colonies in the park.

Discussion

Every C. formosanus and R. flavipes colony in Louis Armstrong Park could be considered non-structurally infesting colonies since only minor and incidental C. formosanus activity was ever found in each of the major structures throughout this four-year study. The majority of trees present in the foraging territories of each C. formosanus colony showed moderate to severe damage, and many trees collapsed during inclement weather because of the extensive feeding to the heartwood, which reduced structural integrity. Many of the same species have been previously listed as commonly attacked living trees by C. formosanus in urban settings (Spink 1967, La Fage 1987, Chambers et al. 1988). It is unclear why six species were not attacked; however, most of these trees were located on small grass islands in the parking lots or were in areas of reduced termite pressure.

With exception to C. formosanus colony # 5 and # 6, the foraging population estimates (avg. 1,909,582) were similar to previously documented estimates for C.

formosanus colonies in urban environments (Su and Scheffrahn 1988b). The estimates for colony # 5 and # 6 (518,913 and 194,132) seemed very low in comparison to other estimates of colony size. This may have been the result of problems encountered during the triple mark-recapture procedure for each colony (Thorne et al. 1996). On the other hand, these may be accurate estimates and the low numbers are reflective of an older colony in decline based on larger mean worker weights (Grace et al. 1995). The negative relationship between mean worker weight and wood consumption rate is supported by the findings of Su and La Fage (1984), whereby colonies with larger workers tend to consume less wood than colonies with small workers. Therefore, C. formosanus colonies in the park with larger workers and lower wood consumption rates may be older colonies in decline. This result would appear to be supported by the findings of Grace et al. (1995). Also, the positive relationship between worker size and foraging territory from C. formosanus colonies in Armstrong Park would suggest older colonies tend to have larger, established foraging territories.

Foraging territories were also similar in total area (from 83 to 1,634 m^2) to C. formosanus colonies from previous reports (King and Spink 1969, Su and Scheffrahn 1988b). The validity of conducting mark-recapture studies to determine the foraging territory of a unique colony was confirmed after DNA fingerprinting analysis for each colony. In recent years, DNA fingerprinting has been used to delineate the foraging territories of C. formosanus in Hawaii (Husseneder and Grace 2001).

Activity within each territory was affected by colder temperatures, as evident in overall wood consumption and UMS activity over time. Other studies have confirmed this seasonality in C. formosanus populations in Louisiana (Waller and La Fage 1987, Delaplane et al. 1991). The amount of rainfall over time (Appendix B) may have reduced activity in many UMSs throughout the park. Near drought conditions were experienced in New Orleans during the year 2000, which most likely lead to an overall reduction in wood consumption and UMS activity in July and August 2000 (Fig. 3-10).

Personal field and laboratory observations of interspecific encounters between workers and soldiers of C. formosanus and R. flavipes always resulted in either immediate aggression or retreat. In this study, R. flavipes colonies present in C. formosanus territories were only found in UMSs after months of C. formosanus inactivity during colder periods of the year. As temperatures rose, and C. formosanus activity returned to the vicinity of the R. flavipes activity, the R. flavipes colony would abandon the UMS within weeks of it becoming active with the C. formosanus colony. Interspecific exclusion of R. flavipes by C. formosanus in urban locations has been documented in southeastern Florida (Su and Scheffrahn 1988b).

It was uncertain whether or not C. formosanus colonies in Louis Armstrong Park would exhibit any type of intercolony aggression. On one occasion during summer 1999, a dead, blue-dyed worker from FST # 4 was recovered in a UMS occupied by nearby FST # 5. This observation has lead to further investigations into possible aggressive interactions among C. formosanus colonies in the park, especially among neighboring colonies. Aggressive behavior between neighboring colonies may help explain why foraging territories were distinct in the park and why there were areas of inactivity between territories.

Table 3-1. Living trees attacked by C. formosanus in Louis Armstrong Park, New Orleans, from May 1998 – August 2001.

Common Name	Species	Family	Total Number in Park	Total Number Infested
American elm	Ulmus americana L.	Ulmaceae	4	4
Baldcypress	Taxodium distichum (L.) Rich.	Cupressaceae	137	44
Black cherry	Prunus serotina Ehrh.	Rosaceae	2	1
Canary Island date palm	Phoenix canariensis Chabaud	Arecaceae	18	4
Chinese parasoltree	Firmiana simplex (L.) Wight	Sterculiaceae	37	3
Chinese tallowtree	Sapium sebiferum (L.) Roxb.	Euphorbiaceae	8	1
Crabapple	Malus angustifolia	Rosaceae	3	3
Crapemyrtle	Lagerstroemia indica L.	Lythraceae	59	4
Green ash	Fraxinus pennsylvanica Marshall	Oleaceae	18	8
Hackberry	Celtis laevigata Willd.	Ulmaceae	1	1
Japanese magnolia	Magnolia x soulangeana	Magnoliaceae	12	3
Jelly palm	Butia capitata (Mart.) Becc.	Arecaceae	10	1
Live oak	Quercus virginiana Mill.	Fagaceae	115	50
White mulberry	Morus alba L.	Moraceae	1	1
Redbud	Cercis canadensis L.	Fabaceae	15	10
Red maple	Acer rubrum L.	Aceraceae	36	34
River birch	Betula nigra (L.) Earl Cully	Betulaceae	11	4
Southern magnolia	Magnolia grandiflora L.	Magnoliaceae	23	4
Southern red oak	Quercus falcata Michx.	Fagaceae	13	3
Sycamore	Platanus occidentalis L.	Platanaceae	132	49
Waxmyrtle	Myrica cerifera L.	Myricaceae	9	2
Water oak	Quercus nigra L.	Fagaceae	32	13
Weeping willow	Salix babylonica L.	Salicaceae	4	3
White oak	Quercus alba L.	Fagaceae	8	1
TOTALS	24 species	17 families	708	251

Table 3-2. Living trees showing no evidence of attack by C. formosanus in Louis Armstrong Park, New Orleans, from May 1998 – August 2001.

Common Name	Species	Family	Total Number in Park	Total Number Infested
Bradford pear	Pyrus calleryana Decne.	Rosaceae	13	0
Ginkgo	Ginkgo biloba L.	Ginkgoaceae	2	0
Jerusalem-thorn	Parkinsonia aculeata L.	Fabaceae	3	0
Tulip poplar	Liriodendron tulipifera L.	Magnoliaceae	2	0
Southern Washingtonia	Washintonia robusta H. Wendland	Arecaceae	25	0
(small palms in planters)	N/A	N/A	8	0
Willow oak	Quercus phellos L.	Fagaceae	24	0
TOTALS	6 species	6 families	77	0

Table 3-3. Coptotermes formosanus colony characteristics after multiple mark-recapture studies in Louis Armstrong Park, New Orleans, from 1998 to 2001.

Colony	Mean worker weight (mg)	Mean soldier weight (mg)	Foraging territory area (m^2)	Wood consumption (px/UMS/day)	Foraging population estimate
1	3.76 +/- .18	3.63 +/- .13	1634	2,304.3 +/- 7,169.2	N = 1,687,365 SE = +/- 227,587
2	3.93 +/- .25	3.64 +/- .22	738	1,489.4 +/- 2,871.4	N = 3,074,205 SE = +/- 320,542
3	4.25 +/- .30	4.22 +/- .32	591	1,310.6 +/- 2,256.7	N = 3,630,541 SE = +/- 1,051,098
4	2.96 +/- .31	2.95 +/- .35	83	4,650.2 +/- 7,994.1	N = 4,487,699 SE = +/- 273,623
5	4.40 +/- .20	4.36 +/- .22	818	2,653.6 +/- 4,480.3	N = 518,913 SE = +/- 54,704
6	4.28 +/- .25	4.11 +/- .18	600	606.1 +/- 643.8	N = 194,132 SE = 26,674
7	3.71 +/- .16	3.42 +/- .16	253	2,837.7 +/- 2,701.6	N = 1,611,795 SE = +/- 403,777
8	3.83 +/- .19	3.83 +/- .13	1186	3,702.9 +/- 6,634.8	N = 1,218,562 SE = +/- 151,175
9	4.54 +/- .22	4.17 +/- .20	506	1,441.8 +/- 1,730.6	N = 1,371,892 SE = +/- 315,243
10	3.17 +/- .17	3.05 +/- .09	505	3,423.8 +/- 3,744.8	N = 2,795,752 SE = 240,632
11	3.59 +/- .21	3.18 +/- .21	724	2,726.1 +/- 2,782.1	N = 1,489,816 SE = +/- 133,261
12	3.35 +/- .13	3.16 +/- .11	248	5,174.8 +/- 2,518.0	N = 383,249 SE = +/- 21,065
13	3.93 +/- .21	3.59 +/- .05	227	2,201.8 +/- 2,137.4	N = 2,360,642 SE = +/- 302,318

Table 3-4. Correlation analysis of C. formosanus colony characteristics in Louis Armstrong Park, New Orleans.

Variables	N	r	F-value	P-value
Worker weight vs. Soldier weight	207	0.8852	745.53	< 0.0001
Worker weight vs. Foraging territory	207	0.3429	27.47	< 0.0001
Worker weight vs. Wood consumption	661	0.1916	25.15	< 0.0001
Foraging territory vs. Wood consumption	661	0.0361	0.89	0.3454

Table 3-5. Season totals of alates recovered from 68 glue traps and a single light trap after dispersal flight monitoring in Louis Armstrong Park, New Orleans.

Termite species	1999	2000	2001	2002
C. formosanus	9,666	7,224	3,342	3,263
R. flavipes	23	25	37	0
R. virginicus	6	6	8	2
I. minor	28	30	13	9
I. snyderi	2	5	7	4

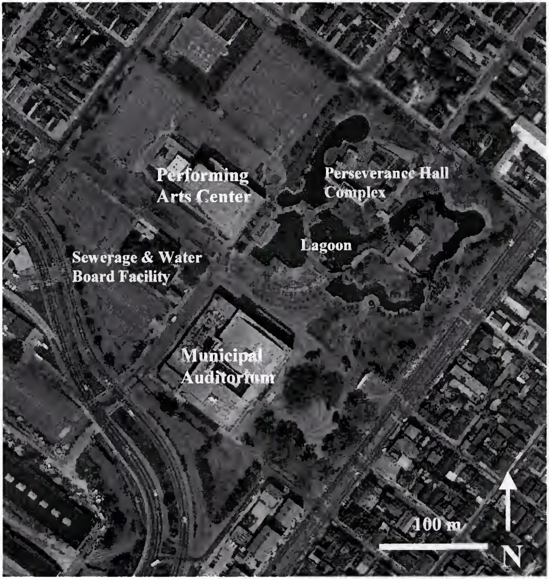

Figure 3-1. Location of major structures and lagoon in Louis Armstrong Park, New Orleans.

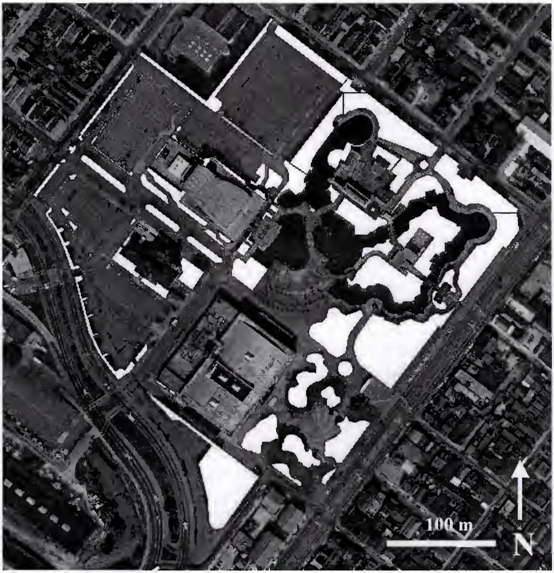

Figure 3-2. Grass areas within Louis Armstrong Park, New Orleans. Total grass area = 3.2 ha.

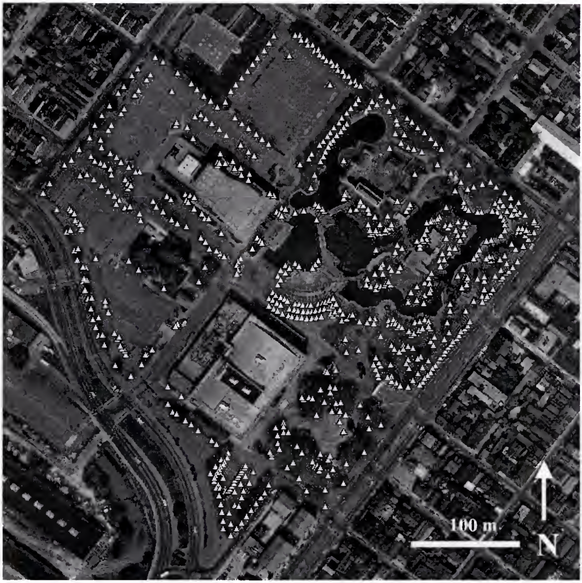

Figure 3-3. Location of all trees in Louis Armstrong Park, New Orleans. Total number of trees = 785.

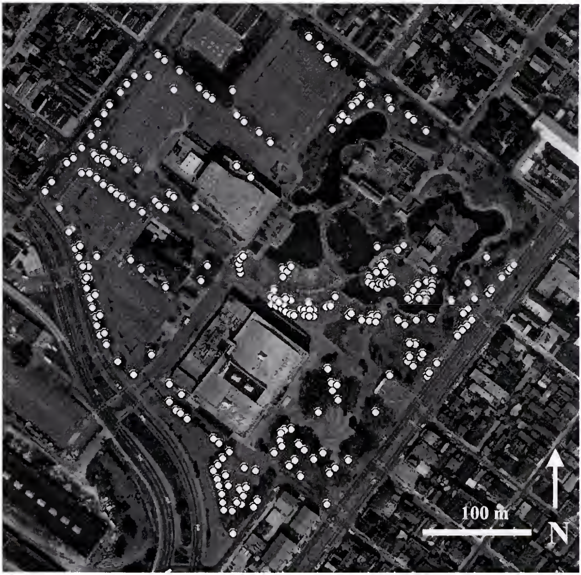

Figure 3-4. Location of living trees attacked by C. formosanus in Louis Armstrong Park, New Orleans, from May 1998 to August 2002.

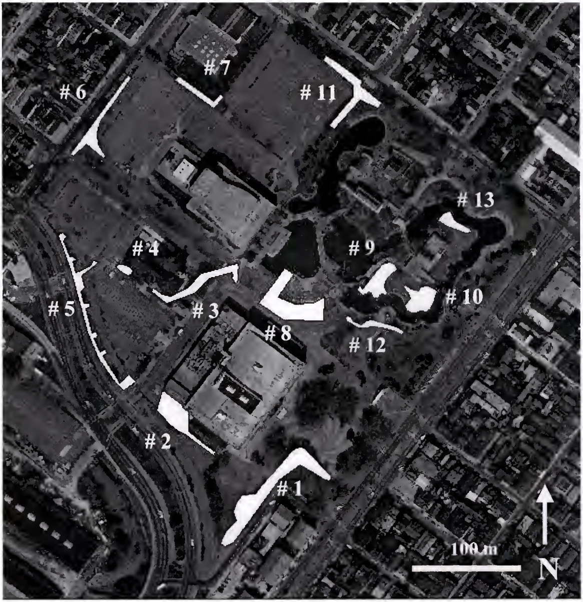

Figure 3-5. Foraging territories of characterized C. formosanus colonies in Louis Armstrong Park, New Orleans, 2001.

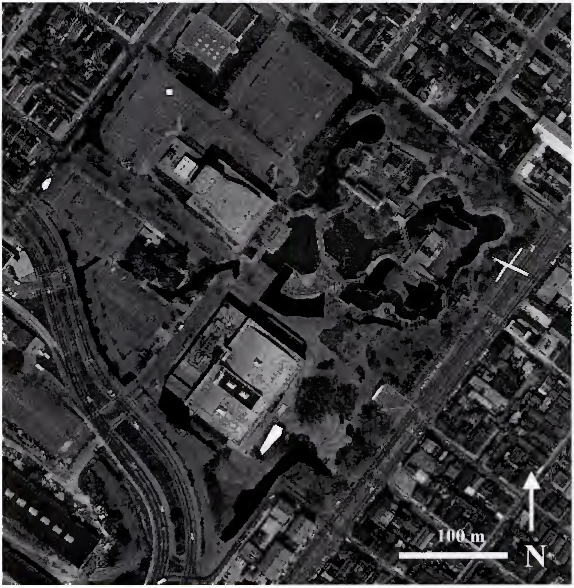

Figure 3-6. Foraging territories of uncharacterized C. formosanus colonies in Louis Armstrong Park, New Orleans, 2001.

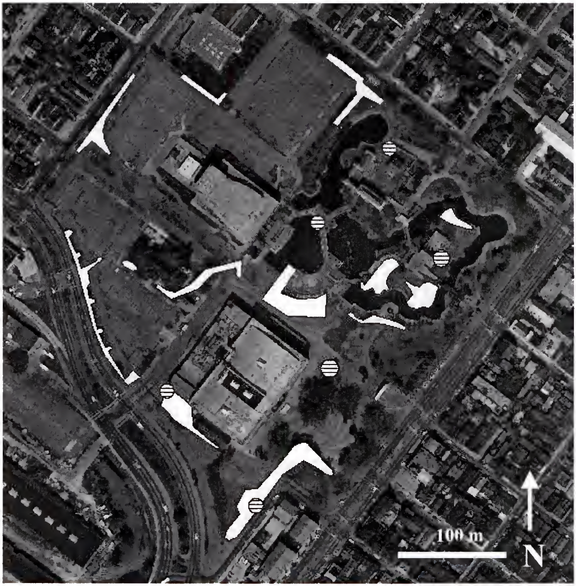

Figure 3-7. Location of R. flavipes activity (lined circles) in Louis Armstrong Park, New Orleans, 2001.

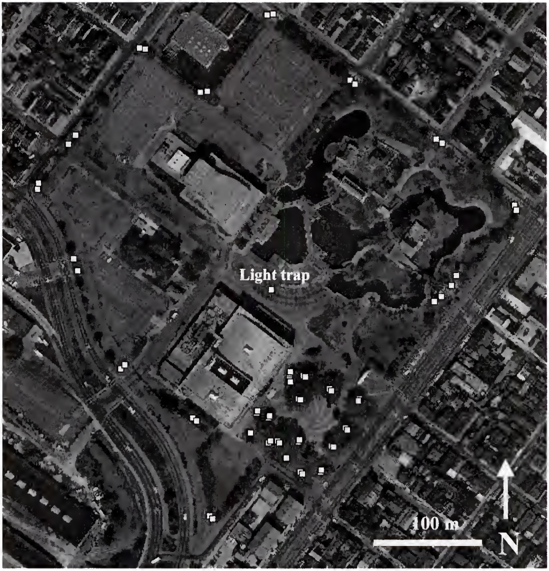

Figure 3-8. Location of 68 glue traps and single light trap for monitoring dispersal flight activity of C. formosanus in Louis Armstrong Park, New Orleans, from 1999 to 2002.

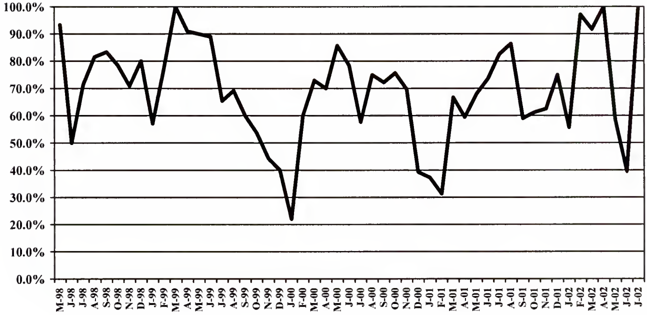

Figure 3-9. Percent of C. formosanus activity in underground monitoring stations (UMSs) over time in Louis Armstrong Park, New Orleans.

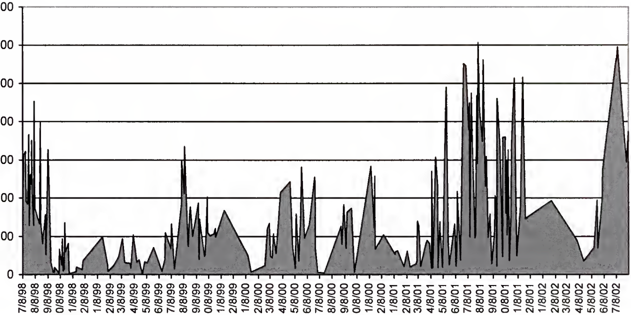

Figure 3-10. Combined C. formosanus wood consumption rate activity in underground monitoring stations (UMSs) over time in Louis Armstrong Park, New Orleans.

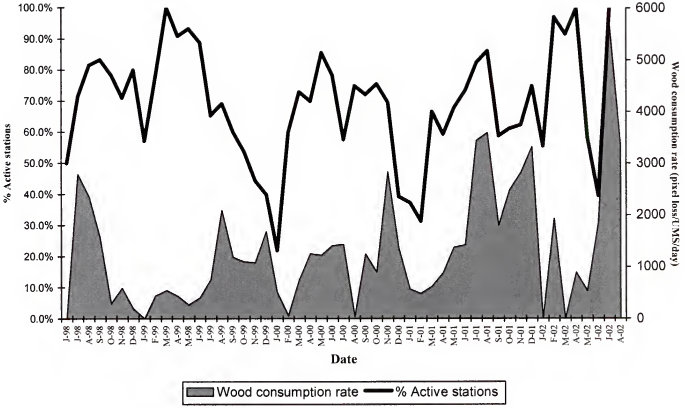

Figure 3-11. Combined C. formosanus percent of UMS activity and wood consumption rate activity in Louis Armstrong Park, New Orleans, from June 1998 to August 2002.

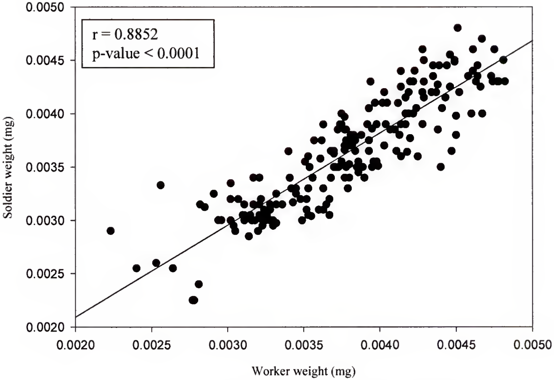

Figure 3-12. Correlation analysis between worker and soldier weights from thirteen C. formosanus colonies.

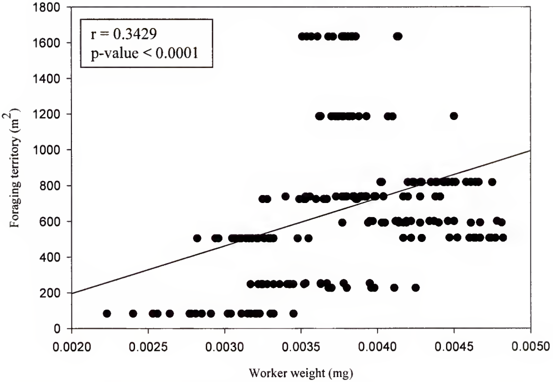

Figure 3-13. Correlation analysis between worker weights and foraging territories from thirteen C. formosanus colonies.

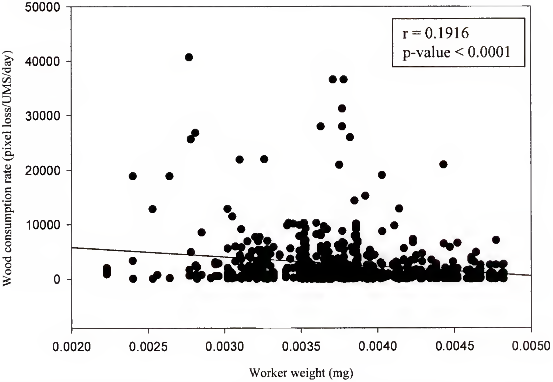

Figure 3-14. Correlation analysis between worker weights and wood consumption rates from thirteen C. formosanus colonies.

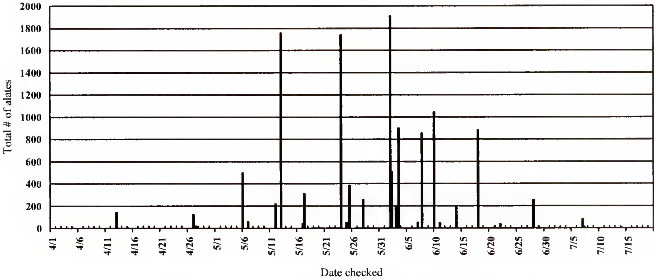

Figure 3-15. Combined number of C. formosanus alates collected by date during dispersal flight monitoring in Louis Armstrong Park, New Orleans, from 1999 to 2002.

CHAPTER 4

AGONISTIC BEHAVIOR BETWEEN COLONIES OF THE FORMOSAN SUBTERRANEAN TERMITE FROM LOUIS ARMSTRONG PARK, NEW ORLEANS, LOUISIANA

Introduction

Inter- and intraspecific agonistic behavior has been one of the most fascinating and least understood behaviors displayed by termites. It is widely known that interspecific interactions usually result in aggressive behaviors, including a wide variety of offensive and defensive reactions (Nel 1968, Thorne 1982, Thorne and Haverty 1991, Shelton and Grace 1996). Many studies have shown that aggressive behavior can be manipulated in termites by washing (Andrews 1911), isolating (Nel 1968), and chilling (Shelton and Grace 1997). Others have correlated interspecific aggression with cuticular hydrocarbon profiles (Haverty and Thorne 1989, Bagneres et al. 1991). In a few cases, intercolony aggression has been used to delineate foraging territories for individual colonies of H. aureus (Jones 1993) and Nasutitermes corniger (Motschulsky) (Isoptera: Termitidae) (Levings and Adams 1984).

However, the recognition mechanism(s) responsible for determining intercolony agonistic behavior is poorly understood, especially among subterranean termites. Lack of intercolony aggression has been observed in populations of R. flavipes (Grace 1996, Bulmer and Traniello 2002) and the Formosan subterranean termite, Coptotermes formosanus (Su and Haverty 1991, Husseneder and Grace 2001). The majority of these studies evaluated agonistic behavior by placing termites from different colonies together in small, open arenas, such as petri dishes (Thorne and Haverty 1991).

Beginning in 1999, intra- and intercolony agonistic behavior bioassays were conducted with eleven C. formosanus colonies located within Louis Armstrong Park, New Orleans, to gain a better understanding of possible recognition mechanisms. All eleven C. formosanus colonies were previously characterized after mark-recapture studies during 1998 and 1999 (Chapter 3). Two different techniques were used to evaluate aggression among these colonies. First, termites from each colony were paired together in the commonly used petri dish arena (non-choice encounter), and second, termites were placed in two-dimensional foraging arenas (choice encounter) and allowed to build foraging tunnels, eventually connecting both territories.

Materials and Methods

Non-choice encounters. Termites from each of the eleven C. formosanus colonies were collected from underground monitoring stations (UMSs) from July to November 1999 and August 2000 (Fig. 4-1). Termites were processed immediately in the laboratory. Half of the termites collected from each colony were fed filter paper (Whatman No. 1) dyed with 0.1% Nile Blue A (w/w) (Fisher Scientific, Pittsburgh, PA), and the other half were fed moistened filter paper for at least six days. Then, one group of eleven dyed (ten workers and one soldier) and non-dyed individuals from each colony was paired with the same number of dyed and non-dyed individuals from one of the eleven colonies, resulting in 121 possible pairings. Each pairing was placed together at the same time on a moistened piece of filter paper in a 1 x 5.3 cm diameter petri dish. These combinations were replicated three times totaling 363 units. The initial agonistic responses (mandible flare and/or insertion, chasing, biting, fleeing, submissiveness) were recorded during each 2-min encounter using a video camera. Video footage of each pairing was reviewed later to determine the number of agonistic events in each encounter. After 2-min, each petri dish was covered and the pairing was kept for 48 hrs at about 27^0C and 90% RH. Then, the number of survivors (dyed and non-dyed) was recorded for each pairing.

Choice encounters. Large numbers of termites from each colony were collected from UMSs from May 2000 to March 2001. Again, termites were processed immediately and fed dyed or non-dyed filter paper for approximately six days before conducting each pairing. Then, pairs of 275 dyed and non-dyed individuals (250 workers and 25 soldiers) from two different colonies were placed inside one of two vials connected to 3 x 180 x 180 mm plastic foraging arenas containing moistened sand (Fig. 4-3). The two vials were attached on top of the arena approximately 100 mm from each other. Each vial contained a small piece of spruce (Picea sp.). After 72 hrs under laboratory conditions, each arena was evaluated for the presence of complete colony mixing, fighting and mixing, and fighting and retreating back to the introduction vials. When possible, the initial behavior between two colonies was observed immediately after contact was made in the foraging tunnels. Each C. formosanus colony was paired with each of the other ten colonies three times totaling 165 units. It was randomly decided which colony was dyed. No individual colony was ever paired three times with only dyed or non-dyed colonies. At least one pairing of termites collected from different UMSs from the same C. formosanus colony was placed together in arenas.

Results

Non-choice encounters. All intracolony pairings resulted in neither aggression nor significant mortality (Table 4-1 and 4-3, Fig. 4-2). There were no observed differences in termite behavior after dye treatments. Initial aggressive responses varied among pairings of different colonies. Various behaviors observed during these trials included soldier mandible flares, mandible insertion (in only a few cases), chasing and fleeing, dominance and submissiveness, and workers biting other workers and soldiers. The majority of these encounters began with one colony becoming the aggressor. It could not be determined which colony seemed to be the dominant aggressor in any of the trials with all colonies because sometimes the same colony would be both an aggressor and a defender. In a few pairings, workers of the aggressor colony would either restrain or clamp another worker with their mandibles for a few seconds and then release the submissive worker relatively unharmed. At the same time, soldiers from the aggressor colony would flare their mandibles immediately when contact was made with members from the other colony and begin chasing these termites around the arena.

Aggression ranged from C. formosanus # 1 and # 7 aggressive towards two different colonies to C. formosanus # 11 aggressive towards eight different colonies. For all colony pairing, each colony was aggressive towards an average of 4.5 colonies (Table 4-1). Overall, C. formosanus # 11 seemed to be the most aggressive colony during each petri dish trial based on total number of aggressive encounters (Table 4-1), combined number of agonistic responses (Table 4-2), and combined mortality associated with each pairing after 48 hrs (Table 4-3).

Mortality after 48 hrs was greatest among pairings where aggressive behavior was initially observed in petri dishes (Table 4-3). Aggression in petri dish encounters did not always result in a large number of combined mortality for all three trials (Table 4-3). In a few cases, combined mortality was high for non-aggressive encounters (Table 4-3). In four situations, only one out of six total pairings between C. formosanus # 2 and # 8, C. formosanus # 3 and # 5, C. formosanus # 7 and # 10, and C. formosanus # 7 and # 6 resulted in aggression, and mortality was minimal and only represents dead termites from that single trial (Tables 4-2 and 4-3).

Choice encounters. All intracolony pairings resulted in neither aggression nor significant mortality (Fig. 4-3). A greater number of aggressive encounters were observed between different colonies during two-dimensional foraging arena trials than during petri dish trials (Table 4-4). Aggression was observed between different colonies during both petri dish and foraging arena trials (Tables 4-4 and 4-5). However, in many cases, aggression was observed only during foraging arena trials and not in petri dish trials (Table 4-6). Colonies during the foraging arena trials displayed aggression towards six to nine other colonies (average 8 aggressive encounters) (Table 4-7).

Observations, including some video footage, on the initial encounter in the arenas revealed immediate attack by the worker caste from one or both colonies. Meetings between different colonies began with workers conducting a behavioral inspection of each other with their antenna. If the meeting was hostile, then one or both workers would begin to bite the antenna, legs, and abdomen of the other. After the initial battle, workers and soldiers would proceed to the area of conflict and pack themselves tightly into the foraging tunnel connection, eventually dying. This behavior was termed "suicide cramming" (Fig. 4-4). At least one incident of suicide cramming was observed in all aggressive foraging arena trials. Then, activity throughout existing tunnels would cease and surviving individuals from each colony would retreat back to their introduction vials (Fig. 4-5). Mortality was not assessed for each trial; however, when each trial was finished and arenas were thoroughly cleaned before the next trial, only a few surviving workers and soldiers were discovered. In a few cases, colony members from both colonies would mix with each other after an initial aggressive encounter.

As the data were analyzed for both trials, it became evident that numerous encounters between different colonies were either aggressive during both trials, only aggressive during one of the trials, or lacked any aggressive behavior in either trial (Table 4-8). The majority of encounters was always aggressive or was only aggressive in foraging arena trials and not petri dish trials (Table 4-8).

Discusssion

As stated in previous studies, it is difficult to explain agonistic behavior and the recognition mechanisms involved during intercolony encounters. This study only evaluated aggressive behavior among C. formosanus colonies in Louis Armstrong Park. Nevertheless, a significant amount of aggression was observed among these eleven colonies, especially in foraging arena trials. Surprising results were obtained by comparing the commonly used petri dish experiment with the two-dimensional foraging arena experiment. It appeared that the foraging arena was a more ecologically relevant bioassay for evaluating initial encounters of different C. formosanus colonies, and was comparable to an actual field situation. As evident in the literature, petri dishes have been used for pair-wise aggressive behavior experiments for various termite species in the past (Nel 1968, Levings and Adams 1984, Clement 1986, Haverty and Thorne 1989, Bagneres et al. 1991, Su and Haverty 1991, Shelton and Grace 1997, Husseneder and Grace 2001, Bulmer and Traniello 2002, Kaib et al. 2002). Few studies have evaluated aggressive behavior in laboratory arenas other than petri dishes (Binder 1988, Grace 1996, Cornelius and Osbrink 2000).

When colonies were aggressive in the petri dish trial, it was expected that they would be aggressive in the foraging arenas, and as a result, about half of the pairings were always aggressive in both test trials (24 different pairings, i.e. colony # 1 vs. # 3) (Table 4-6). At the same time, colonies that were not aggressive in petri dishes were expected to show no aggression in foraging arenas, and a few pairings confirmed this hypothesis (9 pairings, i.e. colony # 1 vs. # 5) (Table 4-6). It was unclear why two colony pairings (# 8 vs. # 11 and # 5 vs. # 11) resulted in aggression during petri dish trials and no aggression in foraging arena trials (non-shaded, marked cells, Table 4-6). The most surprising result was the lack of immediate aggression among 20 colony pairings in petri dishes and the presence of aggressive behavior during foraging arena trials (shaded, non-marked cells, Table 4-6).

In a more confined setting, such as a foraging arena, the presence of possible colony odors becomes evident. Any volatile odors may not be present in sufficient amounts or absent altogether during petri dish trials. There may be a volatile recognition cue present, such as a colony odor, in addition to distinct tactile behaviors, that lead to aggression in foraging arenas and not in petri dishes (Thorne and Haverty 1991). Therefore, the possibility of distinct colony odors seems more appropriate since DNA and cuticular hydrocarbon analyses are not directly correlated with C. formosanus aggressive behavior (Su and Haverty 1991, Husseneder and Grace 2001). This study supports the idea of a colony odor based on the overall number of aggressive encounters among the same colonies in foraging arenas and lack thereof in petri dishes. Although currently unknown, the components of this odor may include a combination of airborne chemical cues emitted from a group of termites sharing their interconnecting galleries. In addition, cuticular hydrocarbons, contact pheromones, and/or volatile airborne chemicals may play a role in colony recognition. The acceptance of workers and soldiers from one colony into another after initial fighting was unexpected. It is unclear why this situation occurred, but these individuals may have acquired the "odor" of the other colony or had similar behavioral responses.

The most interesting result of this study was the aggressive response between neighboring colonies in the park. Many of these neighboring colonies, such as # 3 and # 4 (Fig. 4-1), displayed no aggression during petri dish trials, but were aggressive during foraging arena trials (Table 4-6). This supports the concept of a volatile recognition cue present inside foraging tunnels of different colonies that will elicit an aggressive response towards neighboring colonies. Over time, neighboring colonies may occasionally interact with each other at feeding sites or inside foraging galleries. In a competitive environment with increased interactions, these colonies may have acquired the ability or "learned" to recognize the "odor" of a neighboring colony, which leads to aggression and a fairly stable and well-protected foraging territory. According to Wilson (1971), "Learning apparently plays a key role in the recognition of colony odor, at least among colonies belonging to the same species." For example, neighboring pairs of # 1 and # 2, # 4 and # 5, # 9 and # 10, and # 7 and # 11 fought during foraging arena trials, but did not fight during petri dish trials. Another good example is the results from the pairings of # 4, # 3, and # 8. The neighboring pairs of # 4 and # 3 always fought, # 3 and # 8 always fought, but # 4 and # 8 never fought. Because the foraging territory of # 3 was between these two colonies, the chance encounter of individuals from both # 4 and # 8 coming into contact with each other is unlikely. These two colonies may not recognize the colony odor of the other because of the lack of interaction and exposure over time.

The lack of aggression from distant colonies also supports this possibility. For example, pairings # 6 and # 9, # 1 and # 11, and # 5 and # 8 never exhibited any aggression towards one another throughout both trials. Further research on intercolony recognition is required to describe specific components in a colony odor that may or may not elicit aggressive behavior. It would also be interesting to determine the amount of time required for young, neighboring C. formosanus colonies in the field to develop aggressive behavior towards one another after repeated interactions under both competitive and noncompetitive situations.

Table 4-1. Total number of aggressive encounters of three replicates between eleven *C. formosanus* colonies paired together in petri dish arenas (non-choice encounters). Trials # 1 – 3, 1999 – 2000.

	Non-dyed colony										
Dyed colony	1	2	3	4	5	6	7	8	9	10	11
1	0	0	3	0	0	1	0	0	0	0	0
2	0	0	0	1	2	0	2	0	0	0	2
3	3	0	0	0	0	0	0	3	0	0	2
4	0	1	0	0	0	0	0	0	2	2	3
5	0	2	1	0	0	2	0	0	2	0	3
6	1	0	0	0	2	0	1	2	0	0	3
7	0	1	0	0	0	0	0	0	0	1	0
8	0	1	1	0	0	2	0	0	3	1	1
9	0	0	0	2	1	0	0	2	0	0	1
10	0	0	0	2	0	0	0	1	0	0	2
11	0	1	2	1	2	3	0	1	2	2	0

Table 4-2. Total number of agonistic responses during two-minute encounters in petri dishes between eleven *C. formosanus* colonies. Trials # 1 – 3, 1999 – 2000.

Dyed colony	Non-dyed colony										
	1	2	3	4	5	6	7	8	9	10	11
1	0	0	19	0	0	4	0	0	0	0	0
2	0	0	0	5	26	0	22	0	0	0	20
3	20	0	0	0	0	0	0	20	0	0	15
4	0	7	0	0	0	0	0	0	22	27	30
5	0	8	8	0	0	15	0	0	36	0	16
6	7	0	0	0	14	0	15	20	0	0	20
7	0	8	0	0	0	0	0	0	0	22	0
8	0	13	0	0	0	15	0	0	31	2	3
9	4	0	0	15	4	0	0	18	0	0	4
10	0	0	0	16	0	0	0	4	0	0	21
11	0	6	16	0	12	32	0	4	8	26	0

Table 4-3. Combined mortality associated with agonistic behavior during 48 hr exposures of two ten-member groups from eleven C. formosanus colonies – Trials # 1 – 3. Cells with bold numbers represent initial aggressive behavior in petri dishes.

Dyed colony	Non-dyed colony*										
	1	2	3	4	5	6	7	8	9	10	11
1	0/0	0/0	**14/1**	1/0	1/0	**20/1**	1/0	0/0	2/0	0/0	3/0
2	1/0	0/0	2/0	0/0	**2/0**	0/0	**2/0**	0/1	0/0	0/0	**1/1**
3	**10/1**	2/0	0/0	0/0	13/0	0/0	0/0	**1/0**	0/0	4/0	**29/2**
4	0/0	0/0	10/2	1/0	14/0	2/0	2/0	2/0	**12/0**	**30/1**	**21/2**
5	0/0	0/0	**1/0**	0/0	0/0	**19/2**	0/0	0/0	**10/1**	0/0	0/0
6	**4/1**	0/0	0/0	12/1	0/0	0/0	**4/0**	**27/0**	0/0	8/0	**27/1**
7	0/0	0/0	0/0	0/0	1/0	13/0	0/0	0/0	0/0	**21/1**	2/0
8	1/0	0/0	**1/0**	0/0	20/1	**15/0**	0/0	18/2	**15/0**	**5/2**	**20/0**
9	19/2	2/0	1/0	0/0	**12/1**	0/0	0/0	**11/2**	0/0	10/0	2/0
10	0/0	0/0	9/1	**22/2**	1/0	31/2	14/2	**3/0**	24/0	1/1	**47/0**
11	1/0	0/0	**21/2**	**1/0**	**16/2**	**7/0**	15/0	**11/1**	**37/0**	**10/0**	0/0

*In each cell, the number to the left represents dead workers present after 48 hrs and the number to the right represents dead soldiers.

Table 4-4. Total number of aggressive encounters of three replicates between eleven C. formosanus colonies paired together in two-dimensional foraging arenas (choice encounters). Trials # 1 – 3, 2000 – 2001.

Colony	1	2	3	4	5	6	7	8	9	10	11
1											
2	3										
3	2	3									
4	1	3	3								
5	0	3	3	2							
6	3	1	0	2	3						
7	2	3	2	0	3	3					
8	0	2	3	0	0	2	1				
9	3	2	1	3	3	0	2	3			
10	3	0	3	3	1	3	3	3	2		
11	0	2	2	1	0	3	1	0	3	3	

Table 4-5. Aggressive behavior displayed by eleven C. formosanus colonies during two-minute encounters in petri dishes. Marked cells represent an aggressive response.

Dyed colony	Non-dyed colony										
	1	2	3	4	5	6	7	8	9	10	11
1			X			X					
2				X	X		X				X
3	X							X			X
4		X							X	X	X
5		X	X			X			X		X
6	X				X		X	X			X
7		X								X	
8		X	X			X			X	X	X
9				X	X			X			X
10				X				X			X
11		X	X	X	X	X		X	X	X	

Table 4-6. Aggressive behavior displayed by eleven C. formosanus colonies during 48 h encounters in two-dimensional foraging arenas. Marked cells represent an aggressive response during petri dish trials and shaded areas represent an aggressive response during arena trials.

Dyed	**Non-dyed colony**										
colony	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1		▨	X ▨	▨		X ▨	▨		▨	▨	
2	▨		▨	X ▨	X ▨	▨	X ▨	▨	▨		X ▨
3	X ▨	▨		▨	▨		▨	X ▨	▨	▨	X ▨
4	▨	X ▨	▨		▨	▨			X ▨	X ▨	X ▨
5		X ▨	X ▨	▨		X ▨	▨		X ▨	▨	X
6	X ▨	▨		▨	X ▨		X ▨	X ▨		▨	X ▨
7	▨	X ▨	▨		▨	▨		▨	▨	X ▨	▨
8		X ▨	X ▨			X ▨	▨		X ▨	X ▨	X
9	▨	▨	▨	X ▨	X ▨		▨	X ▨		▨	X ▨
10	▨		▨	X ▨	▨	▨	▨	X ▨	▨		X ▨
11		X ▨	X ▨	X ▨	X	X ▨	▨	X	X ▨	X ▨	

Table 4-7. Total number of aggressive responses for each C. formosanus colony during non-choice (petri dish) and choice (foraging arena) bioassays from 1999 to 2001.

Colony #	# of colonies fought with in petri dish	# of colonies fought with in foraging arena	# of aggressive encounter for both trials
1	2	7	9
2	5	9	14
3	4	9	13
4	4	8	12
5	5	7	12
6	5	8	13
7	3	9	12
8	6	6	12
9	4	9	13
10	4	9	13
11	8	7	15

Table 4-8. Summarized aggressive responses between eleven C. formosanus colonies during non-choice (petri dish) and choice (foraging arena) bioassays from 1999 to 2001.

Aggression in petri dish	Aggression in foraging arena	Number of colony pairings
Yes	Yes	24
No	Yes	20
Yes	No	2
No	No	9

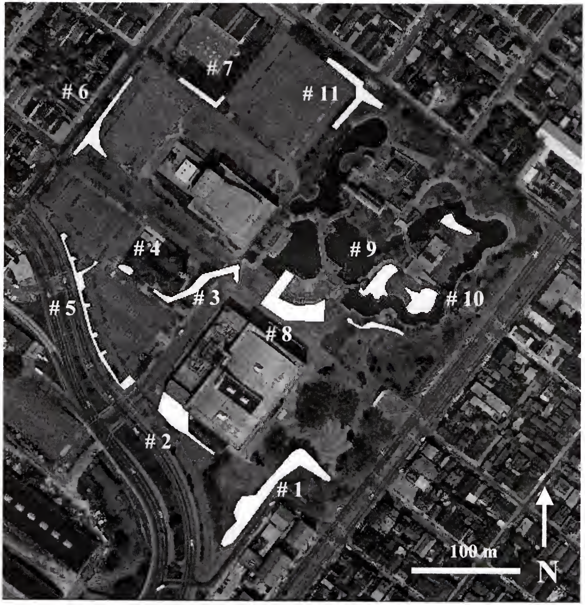

Figure 4-1. Location of eleven C. formosanus colonies from Louis Armstrong Park used in aggressive behavior experiments.

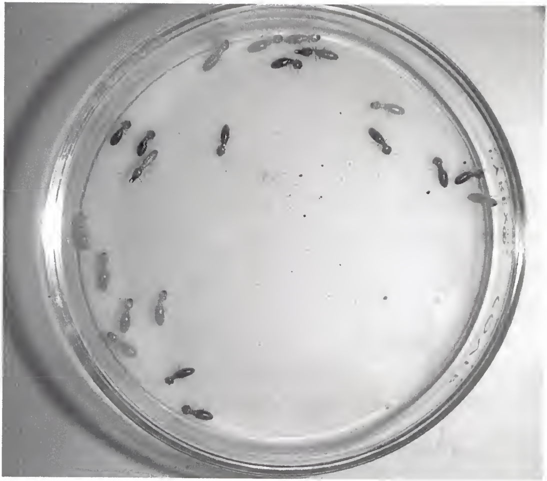

Figure 4-2. Example of C. formosanus colony pairings during petri dish (non-choice) encounters.

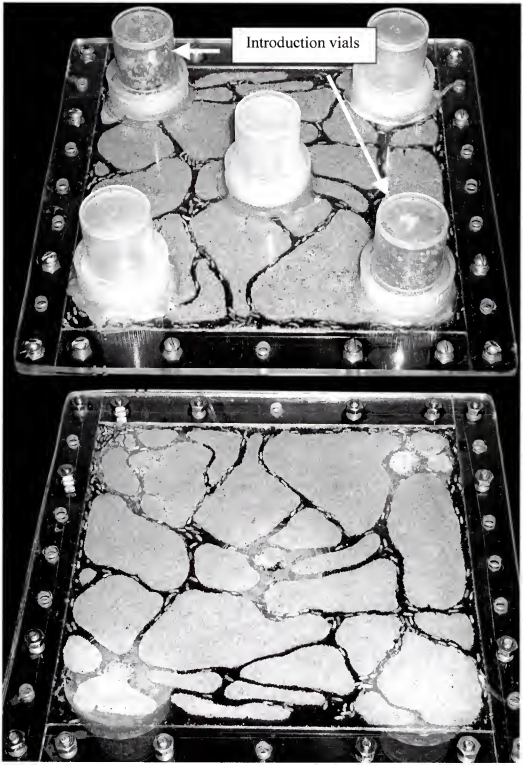

Figure 4-3. Example of a non-aggressive C. formosanus colony pairing during two-dimensional foraging arena (choice) trials when complete mixing and continued foraging occurred.

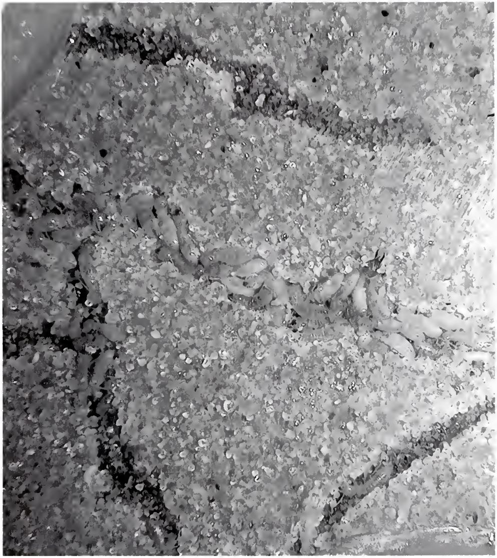

Figure 4-4. Example of "suicide cramming" phenomenon during aggressive C. formosanus colony pairings in two-dimensional arena (choice) encounters.

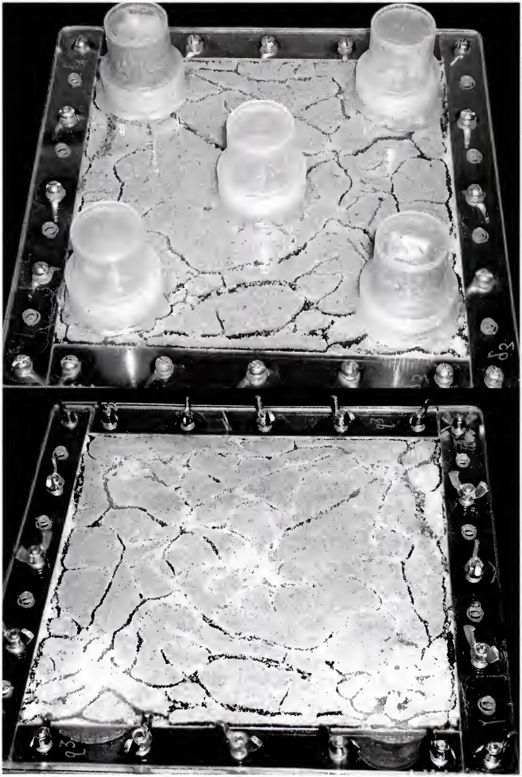

Figure 4-5. Example of an aggressive C. formosanus colony pairing during two-dimensional foraging arena (choice) trials when fighting, “suicide cramming”, and retreating occurred.

CHAPTER 5
SELECTIVE ELIMINATION AND REINVASION OF FORMOSAN SUBTERRANEAN TERMITE COLONIES IN LOUIS ARMSTRONG PARK, NEW ORLEANS, LOUISIANA

Introduction

The Formosan subterranean termite, Coptotermes formosanus, has become one of the most economically important species in the U.S. since its introduction to Hawaii in the early 1900s and the SE U.S. in the 1950s (Su and Tamashiro 1987, Su and Scheffrahn 1990). New baiting technologies have lead to increased efficacy in controlling C. formosanus and other economically important subterranean termite species (Grace et al. 1996, Su and Scheffrahn 1996). Numerous studies have shown the benefits of incorporating the chitin synthesis inhibitor, hexaflumuron, into a baiting strategy to eliminate field populations of the C. formosanus and Reticulitermes spp. (Su 1994, Su and Scheffrahn 1996, Getty et al. 2000). In addition, these field studies documented several occasions where neighboring colonies reoccupy the vacant territories of eliminated colonies. Mark-recapture studies were also part of the criteria involved in determining the foraging territory of each colony and the eventual elimination.

Beginning in 1998, mark-recapture studies were conducted on C. formosanus colonies in Louis Armstrong Park, New Orleans, revealing the presence of over thirteen individual colonies (Chapter 3). At the same time, the U.S. Department of Agriculture – Agricultural Research Service initiated Operation Full Stop; an area-wide termite reduction program focusing on C. formosanus population control in a 15-block area of the French Quarter. Since colony population studies were not conducted in the French Quarter, and it was uncertain whether or not this 15-block area would eventually be reoccupied with new colonies, I decided to evaluate whether or not the elimination of one colony in Armstrong Park would lead to reoccupation by neighboring colonies. In 2001, three well-established and characterized C. formosanus colonies were selected for elimination using 0.5% (wt/wt) hexaflumuron, the active ingredient in the Sentricon® Termite Colony Elimination System (Dow AgroSciences LLC, Indianapolis, IN) (Fig. 5-1). The objectives of this study were to 1) evaluate the use of hexaflumuron to eliminate urban populations of the C. formosanus in New Orleans, and 2) monitor for any reinvasions by established neighboring colonies.

Materials and Methods

In August and September 2000, commercial Sentricon stations were installed in the foraging territories of C. formosanus colony # 2, # 3, and # 9 (Fig. 5-1). These three colonies were chosen for elimination based on their location in relation to nearby characterized C. formosanus colonies. A total of 25 stations were installed in the territory of C. formosanus colony # 2, 17 stations in the territory of C. formosanus colony # 3, and 16 stations in the territory of C. formosanus colony # 9. In several cases, pine stakes (Pinus sp.) harboring C. formosanus activity within each territory were replaced with Sentricon stations. Also, at least one station was installed next to independent, underground monitoring stations (UMSs). Dyed termites were continuously released into each UMS for each colony to connect active stations with active UMSs. Termites were fed filter paper dyed with either Nile Blue A (0.1% w/w), Neutral Red (0.5% w/w), or Sudan Red 7B (0.5% w/w) (Fisher Scientific, Pittsburgh, PA). Because most stations became active with each C. formosanus colony within a week after installation, the wood monitoring devices in each Sentricon station were replaced periodically until actual baiting began in 2001. At the same time, wood consumption rates were continuously calculated after replacing wood feeding blocks in each UMS for each colony (Chapter 3). Every Sentricon station and UMS was checked on a bi-weekly schedule after baits containing hexaflumuron were applied to each colony. Samples from existing colonies, including any new reinvading colonies, were preserved in 100% ethanol for future DNA fingerprinting by C. Husseneder (Univ. of Hawaii).

Foraging territories and UMS and Sentricon station location were mapped on a geo-referenced, aerial orthophoto image (1 pixel = 0.8 square foot) of Louis Armstrong Park using ArcView GIS version 3.1 software (Environmental Systems Research Institute, Inc., Redlands, CA).

Results

Baiting strategies. On June 21, 2001, commercial Recruit II Baitubes (Dow AgroSciences) containing 0.5% hexaflumuron were added to active Sentricon stations located in the foraging territories of C. formosanus colony # 2 (Fig. 5-8), C. formosanus colony # 3 (Figs. 5-14 and 5-15), and C. formosanus colony # 9 (Fig. 5-19). By late August, there was a general decline in Sentricon station and UMS activity, including wood consumption rates, for all three colonies (Figs. 5-2, 5-3, and 5-4). Field observations confirmed colony decline whereby activity within each territory contracted from previously active areas, especially in C. formosanus colony # 2 (Figs. 5-9 and 5-10). Also, the ratio of soldiers and nymphs to workers appeared to increase dramatically and unnaturally in each UMS during the baiting period. All three colonies were considered eliminated by Sept. 17, 2001, approximately three months after baiting began in late June (Figs. 5-2, 5-3, and 5-4). Final bait consumption revealed C. formosanus colony # 2 consumed an equivalent to 12 Baitubes (240 g matrix containing 1,200 mg hexaflumuron), C. formosanus colony # 3 consumed a total of 5.5 Baitubes (110 g matrix containing 550 mg hexaflumuron), and C. formosanus colony # 9 consumed a total of 9 Baitubes (180 g matrix containing 900 mg hexaflumuron). UMS activity had decreased to the point where only one UMS was active for each colony, and usually nymphs and soldiers were the only caste present. The few workers present appeared very sluggish. After elimination, inactive UMSs contained decaying termite bodies and a large number of active collembolans (Insecta: Collembola). On October 4, 2001, trees, which had been actively and consistently harboring these three colonies for over three years, were inspected internally for termite activity using a video borescope (Everest VIT, Inc., Slidell, LA) after drilling a 9.525 mm hole into each tree. As a result, every tree was devoid of termite activity and the interior cavities contained large numbers of collembolans.

Reinvasion studies. Before the elimination of C. formosanus colony # 2 and # 9 occurred, there was new C. formosanus activity in Sentricon stations and UMSs along the perimeter of each foraging territory. Bait was not added to these previously inactive stations for two reasons. First, blue-dyed individuals from C. formosanus colony # 13 were recovered in a single station in the territory of Neutral Red-dyed C. formosanus colony # 9 (Fig. 5-20). In the territory of C. formosanus colony # 2, there was a noticeable difference in mean worker size between the unknown, reinvading C. formosanus colony (3.57 +/- 0.11 mg) and C. formosanus colony # 2 (3.93 +/- 0.25 mg).

Secondly, each baited colony was in decline and the ratio of soldiers and nymphs to workers was very high, and reinvaded stations contained mostly very active workers. Interestingly, a Sentricon station became active with R. flavipes during the decline of C. formosanus colony # 2 in August 2002 (Fig. 5-10). When C. formosanus colony # 2 was eventually eliminated, the reinvading C. formosanus colony slowly reoccupied Sentricon stations and UMSs over time (Figs. 5-11 and 5-12). By August 2002, the new, uncharacterized C. formosanus colony had reinvaded a majority of the vacated territory (Fig. 5-13). The R. flavipes colony remained active in the Sentricon station, even when the new colony reoccupied an adjacent UMS (Fig. 5-13). Wood consumption rate and overall station activity of the C. formosanus colony # 2 reinvader steadily increased after Sept. 2001 (Fig. 5-5).

A similar situation occurred in the foraging territory of C. formosanus colony # 9. Characterized C. formosanus colony # 13 initially reinvaded a single Sentricon station and then foraged further into the foraging territory of eliminated C. formosanus colony # 9, until C. formosanus colony # 13 had reoccupied the entire foraging territory by August 2002 (Figs. 5-20, 5-21, and 5-22). This new activity was reflective in station activity and wood consumption rate (Fig. 5-7).

The decline and eventual elimination of C. formosanus colony # 3 occurred throughout the entire foraging territory at about the same time (Fig. 5-16). The entire foraging territory of C. formosanus colony # 3 remained inactive until March 14, 2002, when new C. formosanus activity was detected in Sentricon stations and UMSs (Fig. 5-17). Again, even though C. formosanus colony # 3 was eliminated, the workers from the new, reinvading C. formosanus colony were very small (2.71 +/- 0.05 mg) in comparison to C. formosanus colony # 3 (4.25 +/- 0.3 mg). By August 2002, the new C. formosanus colony had reoccupied the entire vacated territory, including Sentricon stations and UMSs (Figs. 5-6 and 5-18).

DNA fingerprinting analysis confirmed genetic differences in all baited FST colonies and reinvading C. formosanus colonies (C. Husseneder, Univ. of Hawaii, unpublished data). As of August 2002, there were at least 15 individual C. formosanus colonies in Louis Armstrong Park, including at least six R. flavipes colonies (Fig. 5-23).

Discussion

A relatively small amount of hexaflumuron (approximately 550 to 1,200 mg) was needed to eliminate all three colonies in the park, which was similar to previous reports by Su (1994). After elimination, field observations of previously infested trees within the territories of these three colonies apparently began healing by closing any outer openings maintained by the invading colony for over three years. The effectiveness of using hexaflumuron to eliminate tree-infesting C. formosanus colonies was confirmed during this study.

It is unclear why the reinvading C. formosanus colonies of # 2 and # 3 were not detected before initiating the baiting/elimination program. These may have been young colonies with limited foraging territories and food resources. C. formosanus colony # 2 and/or # 3 may have displayed aggression towards these neighboring colonies, thus preventing colony fusion or invasion (Chapter 4). Only one case of C. formosanus colony fusion has been confirmed using mark-recapture studies (Su and Scheffrahn 1988a). Therefore, the decline in each C. formosanus colony may have reduced the ability of each colony to defend established food sources and tunneling systems, especially in the case of the R. flavipes colony reinvading the territory of declining C. formosanus colony # 2. In southeastern Florida, R. flavipes colonies are commonly displaced by the more aggressive C. formosanus in urban locations (Su and Scheffrahn 1988b). Trail pheromones from an established colony may dissipate quickly inside foraging tunnels, especially when the overall worker population declines as a result of the treatment. The ability of the soldier caste to defend the territory may also be affected because of a reduction in the total worker population after bait application, particularly when the soldier caste relies on workers for feeding and grooming.

New Orleans is considered a city with extremely high termite pressure because of the presence of C. formosanus and its ability to utilize virtually any material containing cellulose. The result of eliminating one colony in a structure or area may lead to further reinvasions by neighboring and opportunistic C. formosanus and/or R. flavipes colonies. Results from this study have shown how only a relatively short time (days before elimination) is needed for one colony to begin reoccupying a vacated territory and continue feeding on the same food sources, such as UMSs and bait stations. As stated by Su (2003a), the elimination of C. formosanus populations in an area the size of a city block in New Orleans can lead to potential reinvasion by neighboring C. formosanus colonies. Some of the benefits of using a baiting system and establishing active monitoring stations within a foraging territory include treatment and future monitoring of new colonies, which may, in all probability, use the same tunneling system connecting stations. This study confirms and reflects the findings of Grace et al. (1996) and Su (2003b) in that the establishment of active monitoring stations and their connections using mark-recapture studies was essential in evaluating and developing short- and long-term control strategies for subterranean termites in Louis Armstrong Park.

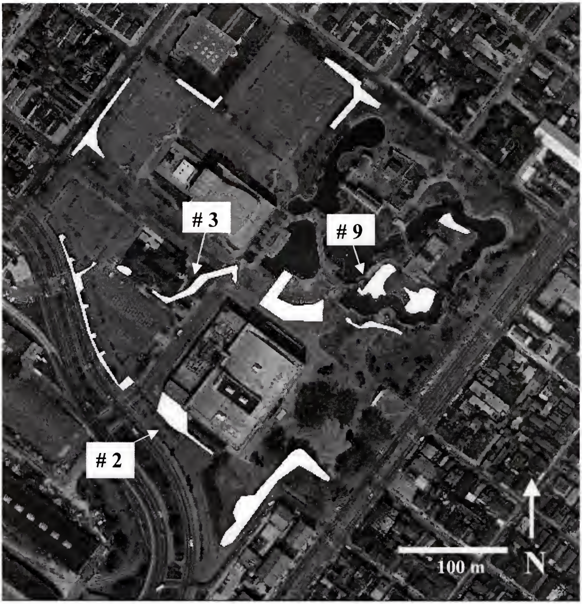

Figure 5-1. Location of three C. formosanus colonies selected for elimination in Louis Armstrong Park, New Orleans, in June 2001.

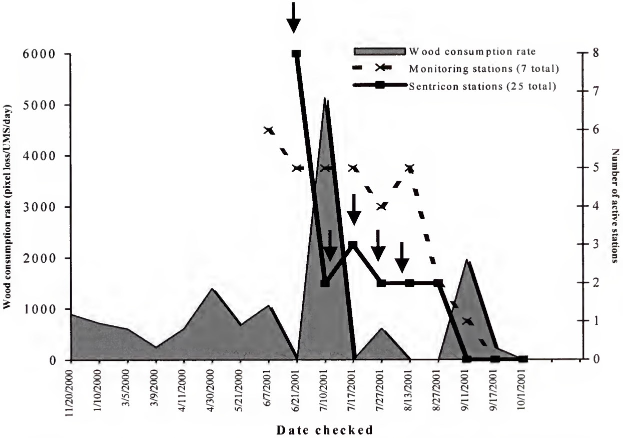

Figure 5-2. Wood consumption rate, baiting history, and UMS and bait station activity of C. formosanus colony # 2 in Louis Armstrong Park, New Orleans, from November 2000 to October 2001. Arrows indicate application of bait toxicant.

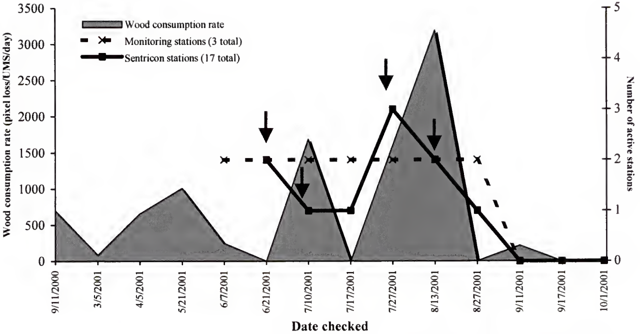

Figure 5-3. Wood consumption rate, baiting history, and UMS and bait station activity of C. formosanus colony # 3 in Louis Armstrong Park, New Orleans, from September 2000 to October 2001. Arrows indicate application of bait toxicant.

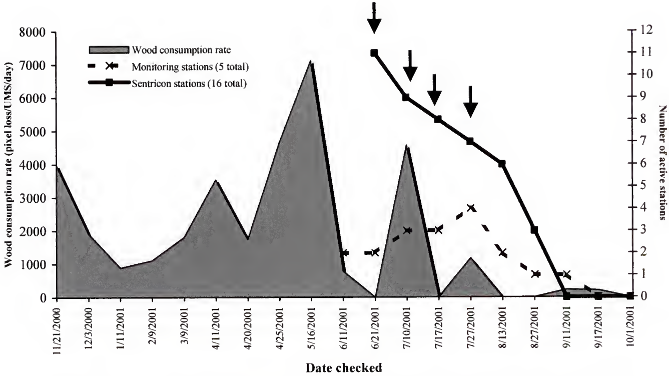

Figure 5-4. Wood consumption rate, baiting history, and UMS and bait station activity of C. formosanus colony # 9 in Louis Armstrong Park, New Orleans, from November 2000 to October 2001. Arrows indicate application of bait toxicant.

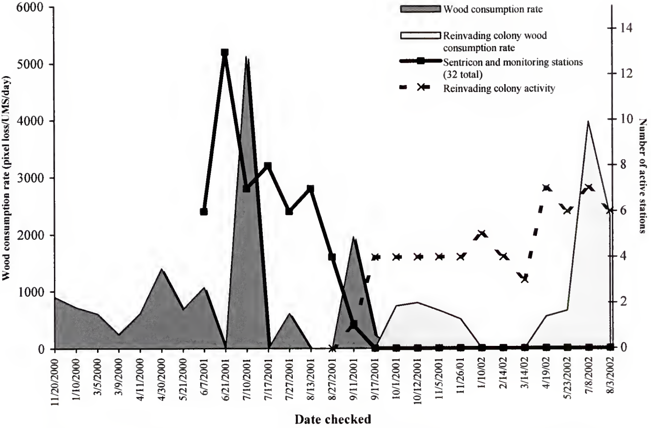

Figure 5-5. Reinvading colony activity inside foraging territory and monitoring stations of eliminated C. formosanus colony # 2 in Louis Armstrong Park, New Orleans, from September 2001 to August 2002.

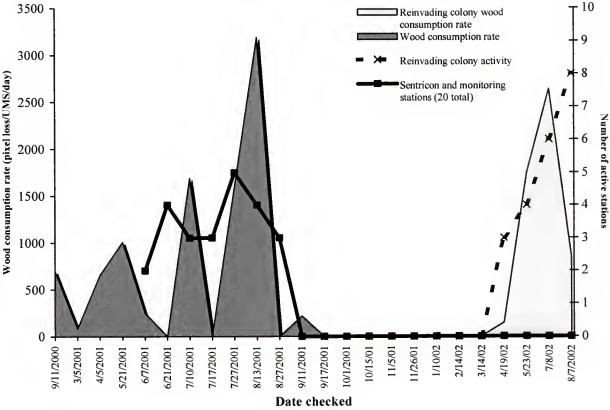

Figure 5-6. Reinvading colony activity inside foraging territory and monitoring stations of eliminated C. formosanus colony # 3 in Louis Armstrong Park, New Orleans, from March 2002 to August 2002.

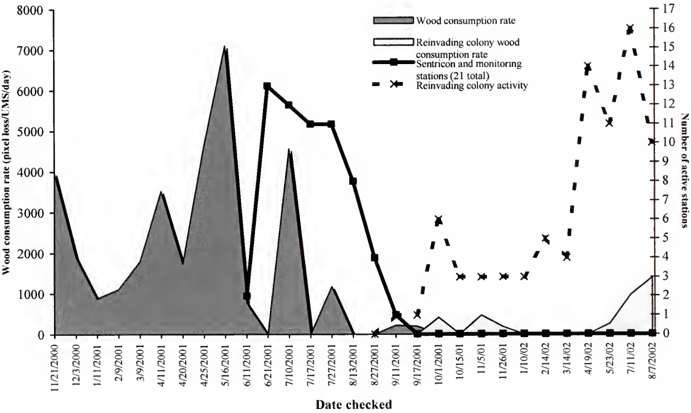

Figure 5-7. Reinvading colony activity inside foraging territory and monitoring stations of eliminated C. formosanus colony # 9 in Louis Armstrong Park, New Orleans, from September 2001 to August 2002.

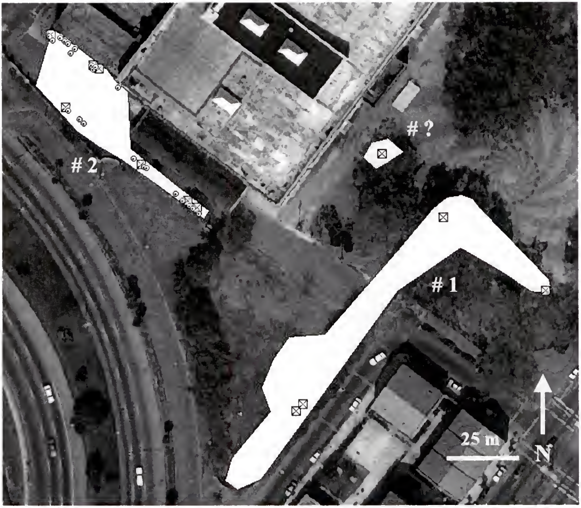

Figure 5-8. Coptotermes formosanus colony # 2 foraging territory in Louis Armstrong Park, New Orleans, from June 1998 to June 21, 2001. Bait introduced on June 21, 2001. Squares represent UMS location and small, doted circles represent bait station location. Foraging territory area for each colony includes UMSs, bait stations, infested trees, and pine stakes connected via dyed individuals.

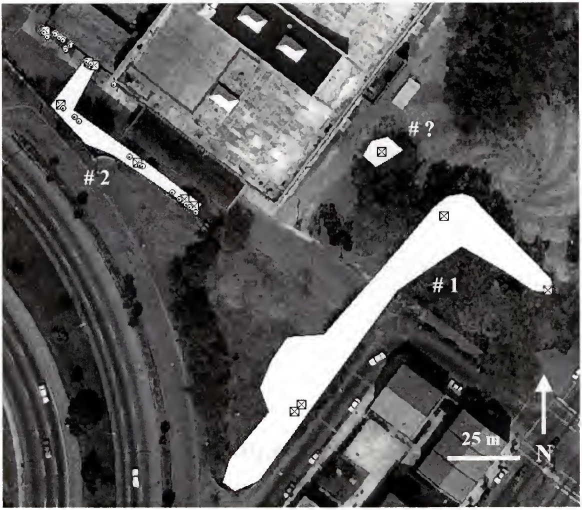

Figure 5-9. Change in C. formosanus colony # 2 foraging territory from June 21 to July 10, 2001. Squares represent UMS location and small, doted circles represent bait station location.

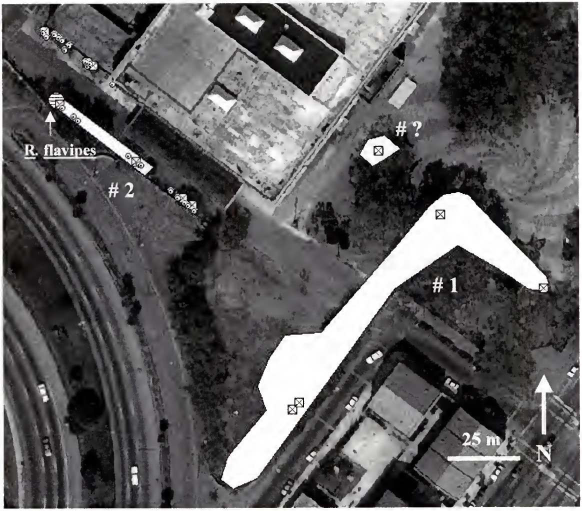

Figure 5-10. Change in C. formosanus colony # 2 foraging territory from July 10 to August 13, 2001. Squares represent UMS location and small, doted circles represent bait station location.

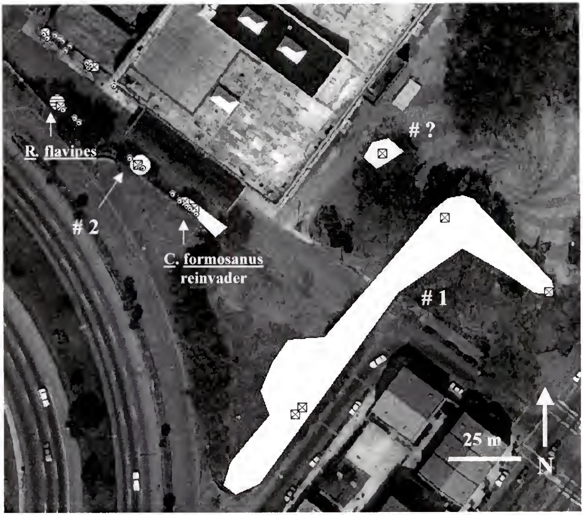

Figure 5-11. Change in C. formosanus colony # 2 foraging territory from August 13 to October 1, 2001, and the location of a reinvading, neighboring C. formosanus colony. Squares represent UMS location and small, doted circles represent bait station location.

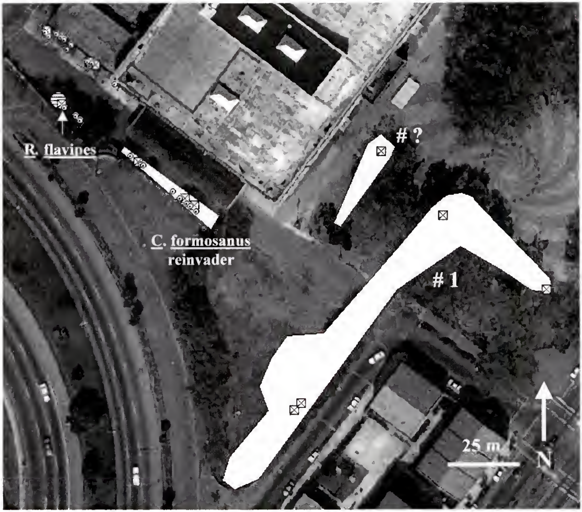

Figure 5-12. Elimination of C. formosanus colony # 2 and movement of reinvading C. formosanus colony into vacated territory from October 1, 2001, to July 8, 2002. Squares represent UMS location and small, doted circles represent bait station location.

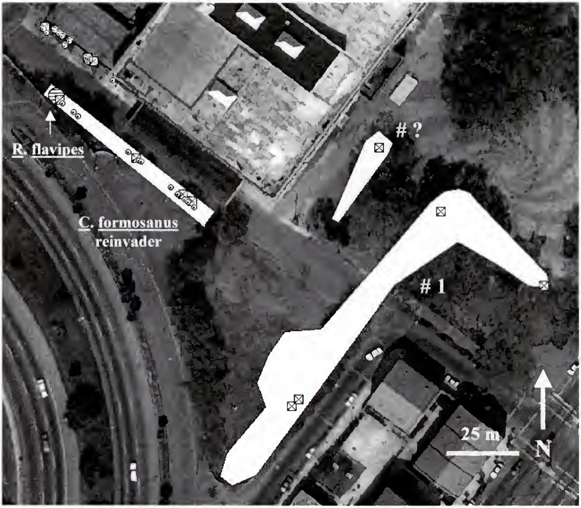

Figure 5-13. Further movement of reinvading C. formosanus colony into vacated territory of eliminated C. formosanus colony # 2 from July 8 to August 2, 2002. Squares represent UMS location and small, doted circles represent bait station location.

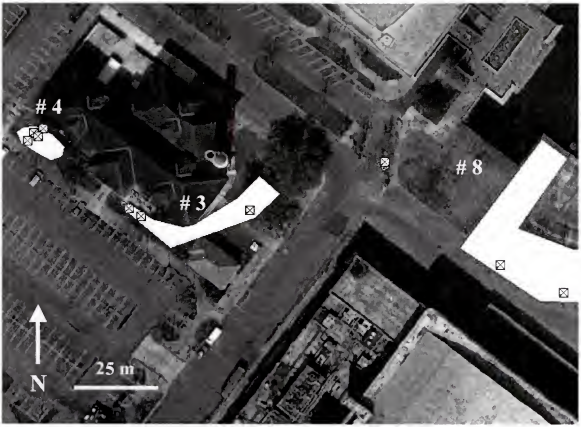

Figure 5-14. Coptotermes formosanus colony # 3 foraging territory in Louis Armstrong Park, New Orleans, from July 21, 1998 to June 21, 2001. Bait introduced on June 21, 2001. Squares represent UMS location and small, doted circles represent bait station location. Foraging territory area for each colony includes UMSs, bait stations, infested trees, and pine stakes connected via dyed individuals.

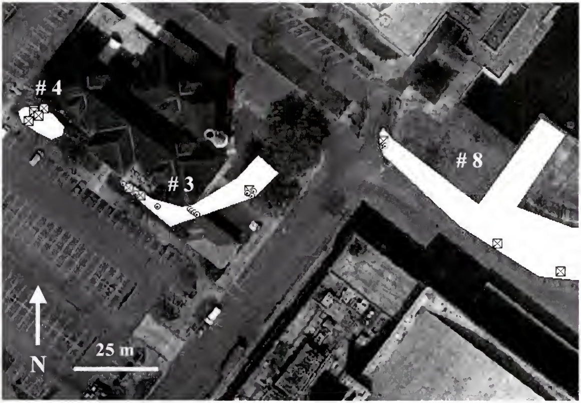

Figure 5-15. Coptotermes formosanus colony # 3 foraging territory from June 21 to August 27, 2001. Squares represent UMS location and small, doted circles represent bait station location.

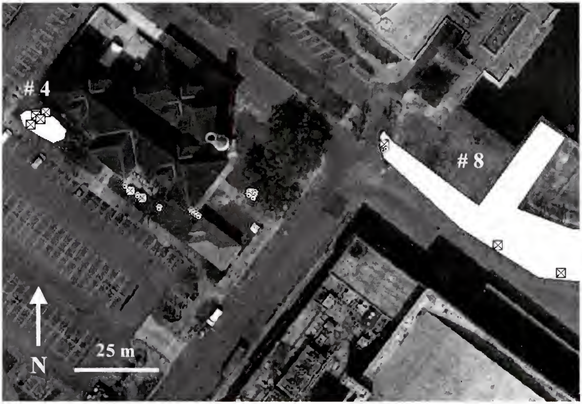

Figure 5-16. Elimination of C. formosanus colony # 3 and vacated territory from August 27, 2001, to March 14, 2002. Squares represent UMS location and small, doted circles represent bait station location.

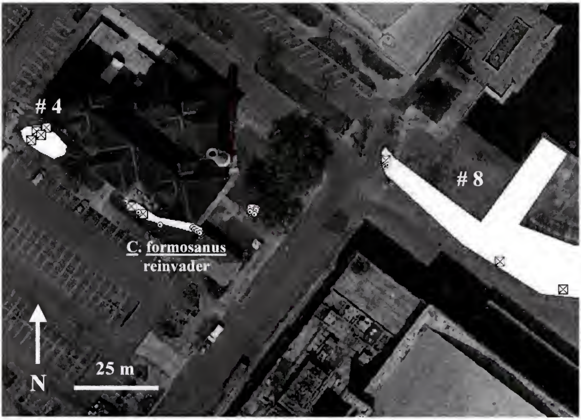

Figure 5-17. New C. formosanus colony reinvading the foraging territory of eliminated C. formosanus colony # 3 from March 14 to July 8, 2002. Squares represent UMS location and small, doted circles represent bait station location.

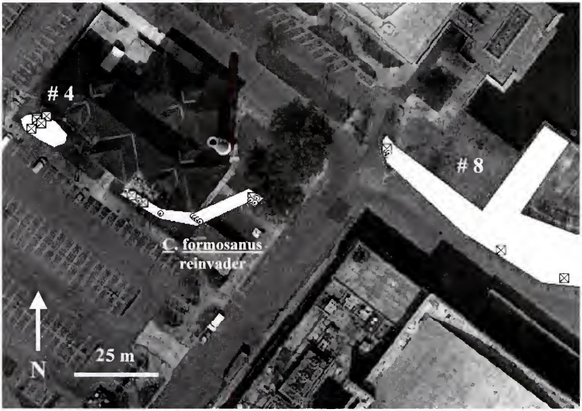

Figure 5-18. Further movement of new C. formosanus colony into vacated territory of eliminated colony # 3 from July 8 to August 7, 2002. Squares represent UMS location and small, doted circles represent bait station location.

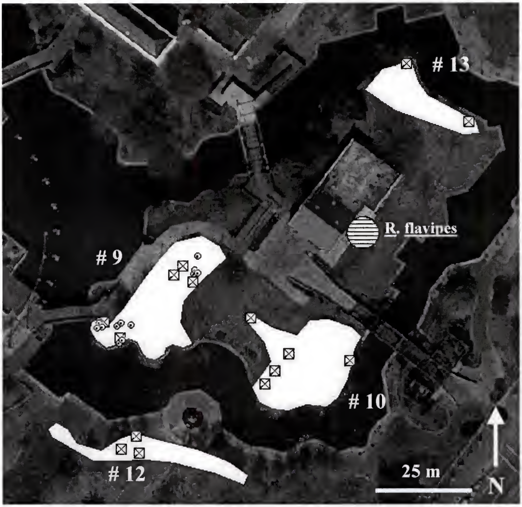

Figure 5-19. Coptotermes formosanus colony # 9 foraging territory in Louis Armstrong Park, New Orleans, from June 1998 to June 21, 2001. Bait introduced on June 21, 2001. Squares represent UMS location and small, doted circles represent bait station location. Foraging territory area for each colony includes UMSs, bait stations, infested trees, and pine stakes connected via dyed individuals.

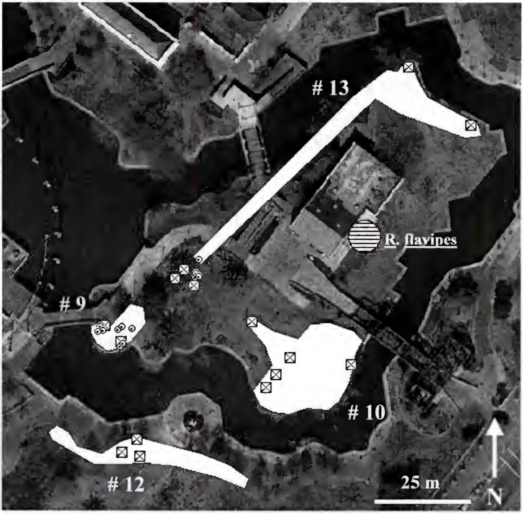

Figure 5-20. Change in C. formosanus colony # 9 foraging territory and reinvasion by C. formosanus colony # 13 from June 21 to September 11, 2001. Squares represent UMS location and small, doted circles represent bait station location.

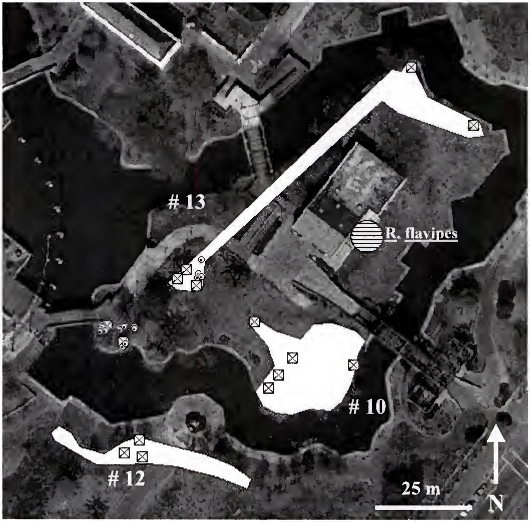

Figure 5-21. Elimination of C. formosanus colony # 9 and further reinvasion by C. formosanus colony # 13 from September 11, 2001 to March 14, 2002. Squares represent UMS location and small, doted circles represent bait station location.

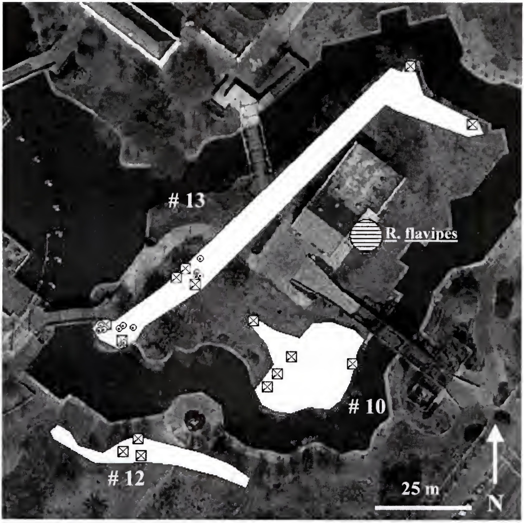

Figure 5-22. Further movement of C. formosanus colony # 13 into vacated territory of eliminated colony # 9 from March 14 to August 2, 2002. Squares represent UMS location and small, doted circles represent bait station location.

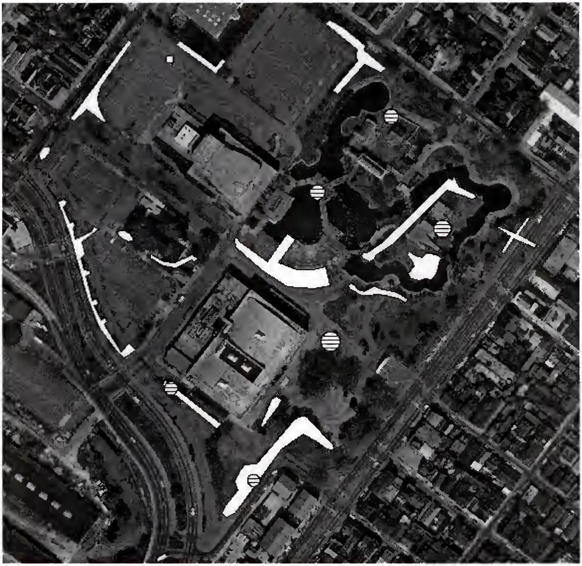

Figure 5-23. Location of all C. formosanus and R. flavipes colonies (lined circles) in Louis Armstrong Park, New Orleans, in August 2002.

CHAPTER 6
CONCLUSION

Since the introduction of the C. formosanus to New Orleans after World War II, it has become increasingly important to prevent any further spread throughout Louisiana and surrounding states. Any successful prevention and elimination program should rely on monitoring the inter- and intrastate movement of infested materials, in addition to incorporating all available resources into control measures in currently infested areas. For any control measure to be effective, basic biological research is needed to understand the colony dynamics and behavior of C. formosanus under field and laboratory conditions.

In this study, an area densely populated with C. formosanus in New Orleans was first examined using mark-recapture studies before any further behavioral or control research was conducted. The actual number of C. formosanus colonies and their foraging territories would not have been detected and overall activity may have been either over- or underestimated if mark-recapture studies were not conducted beforehand. Also, evaluating control measures would have been difficult since neighboring colonies reinvaded the territories of treated colonies in a relatively short period of time. As a result of mark-recapture studies, thirteen well-established C. formosanus colonies were identified and their foraging territories delineated. The efficacy of the baiting strategies implemented in the park was successful once established activity was determined for each C. formosanus colony.

The agonistic behavior experiment shed new light on aggressive behavior among neighboring C. formosanus colonies. A better understanding of why C. formosanus colonies maintain distinct foraging territories was gained by using the two-dimensional foraging arena bioassay. At the same time, more questions arose about which specific mechanisms are responsible for initiating aggressive behavior. It would seem logical that neighboring colonies would protect their food resources and tunneling system by aggressively defending against neighboring colonies, suggesting a distinct intraspecific colony odor. This was, in part, confirmed by each individual study in the park.

The elimination of three C. formosanus colonies created a “mini-vacuum” in the park. These vacated territories, including food sources and existing tunneling system, were completely reoccupied within a year. This result also confirmed how densely and over-populated the area was with C. formosanus and R. flavipes colonies. Future research involving an area-wide termite elimination project, possibly in Louis Armstrong Park, would determine the length of time required for C. formosanus and R. flavipes alate pairs to re-establish inside a much larger “vacuum”. Based on the number of C. formosanus alates recovered year after year, and the presence of small, undiscovered colonies, the probability of this territory becoming completely reoccupied in a few years is relatively high.

APPENDIX A
LETTER OF PERMISSION

Entomology and Nematology Dept.
University of Florida
970 Natural Area Dr.
Gainesville, FL 32611

May 30, 2003

Dr. Richard Baranowski
IFAS/UF
18905 SW 280th Street
Homestead, FL 33031-3314

Dear Dr. Baranowski:

I recently published a paper in late 2002 entitled "Current distribution of the Formosan subterranean termite and other termite (Isoptera: Rhinotermitidae, Kalotermitidae) species in Louisiana", in *Florida Entomologist* Vol. 85, No. 4, pp. 580-587. I am requesting permission to reuse this paper in my dissertation. Your assistance is greatly appreciated and I thank you in advance.

Sincerely,

Matt Messenger

Matt Messenger

APPENDIX B
RAIN GAUGE DATA

Date Of Rain Event	Date Checked	mm	Comments
6/7/1998	6/8/1998	43	
6/21/1998	6/22/1998	59	
6/25/1998	6/26/1998	20	
6/26/1998	6/29/1998	4	
7/7/1998	7/8/1998	4	
7/14/1998	7/14/1998	9.5	
7/16/1998	7/17/1998	10	
7/21/1998	7/22/1998	2	
7/22/1998	7/23/1998	60.5	
7/23/1998	7/24/1998	8	
7/24 - 7/26/98	7/27/1998	29	
7/28/1998	7/29/1998	20	
8/6/1998	8/6/1998	1	
8/9/1998	8/10/1998	14	
8/11/1998	8/12/1998	3.5	
8/12/1998	8/13/1998	11.5	
8/13 - 8/16/98	8/17/1998	5	
8/18/1998	8/19/1998	12	
8/19/1998	8/20/1998	2	
8/21 - 8/22/98	8/24/1998	100	rained all day 8/21
9/1/1998	9/2/1998	54	rained all day 9/1, including weekend
9/6 - 9/7/98	9/8/1998	34	
9/8/1998	9/9/1998	3	
9/10 - 9/12/98	9/12/1998	>136	gauges full; maybe 50 – 70 mm more
9/12 - 9/13/98	9/15/1998	100	9/10 - 9/13 hurricane Francis rain
9/18 - 9/19/98	9/21/1998	48	
9/27 - 9/28/98	9/30/1998	26	hurricane Georges rain
10/7/1998	10/8/1998	30	
11/2/1998	11/2/1998	14.5	
11/11 - 11/12/98	11/13/1998	20	
11/14 - 11/16/98	11/16/1998	50	
12/7/1998	12/7/1998	8	
12/8/1998	12/9/1998	8.5	
12/11 - 12/12/98	12/14/1998	10	
12/27 - 12/29/98	12/30/1998	32	
1/3 - 1/5/99	1/6/1999	12	
1/7/1999	1/8/1999	1	
1/9 - 1/10/99	1/11/1999	46	

1/22/1999	1/25/1999	4.5	
2/20 - 2/21/99	2/22/1999	2	
2/27/1999	3/1/1999	8	
3/2/1999	3/4/1999	9	
3/9/1999	3/9/1999	4.5	
3/13/1999	3/15/1999	41	
3/30/1999	3/31/1999	64.5	
5/11 - 5/12/99	5/12/1999	51	
5/12/1999	5/13/1999	6	
5/30 - 5/31/99	6/1/1999	48	
6/6/1999	6/7/1999	trace	
6/10/1999	6/11/1999	3.25	
6/11 - 6/13/99	6/14/1999	105.5	
6/14/1999	6/15/1999	7	
6/15/1999	6/16/1999	1.75	
6/21/1999	6/22/1999	18	
6/26 - 6/27/99	6/28/1999	98	
7/4 - 7/6/99	7/7/1999	12	
7/8/1999	7/8/1999	20.5	
7/10/1999	7/12/1999	3	
7/13/1999	7/14/1999	15.5	
7/19/1999	7/20/1999	7.75	
7/21/1999	7/22/1999	2	
8/9/1999	8/10/1999	62	
8/10/1999	8/11/1999	3	
8/12/1999	8/13/1999	trace	
8/23/1999	8/24/1999	33	
8/25/1999	8/25/1999	16.5	
9/6/1999	9/7/1999	52	
9/8/1999	9/9/1999	18	
9/28 - 9/29/99	9/30/1999	10	
10/8 - 10/10/99	10/11/1999	68	
10/30 - 10/31/99	11/1/1999	25	
11/21/1999	11/22/1999	2	
12/9/1999	12/9/1999	5	
12/18 & 12/20/99	12/21/1999	58	
1/3/2000	1/4/2000	11	
1/8 - 1/9/00	1/10/2000	7.5	
1/23/2000	1/24/2000	22	
1/28 & 1/29/00	1/31/2000	19	
2/13/2000	2/14/2000	6	
3/15/2000	3/16/2000	7	
3/18 & 3/19/00	3/23/2000	34	
3/27/2000	3/27/2000	8	
4/3/2000	4/4/2000	26	
5/5/2000	5/9/2000	6	

5/19 & 5/20/00	5/22/2000	32	
6/4 & 6/5/00	6/5/2000	20	
6/15, 6/17, & 6/18/00	6/19/2000	58	
6/20/2000	6/22/2000	13	
6/27 & 6/28/00	6/28/2000	15.5	
6/29/2000	6/30/2000	11	
7/1/2000	7/3/2000	4	
7/22/2000	7/24/2000	5	
7/28 & 7/30/00	7/31/2000	7	
7/31/2000	8/1/2000	4.3	
8/1/2000	8/2/2000	21	
8/3 & 8/4/00	8/5/2000	22	
8/10/2000	8/11/2000	22.5	
8/14/2000	8/15/2000	2	
8/29/2000?	8/30/2000	14	
9/4 & 9/5/00	9/6/2000	4.9	
9/9 & 9/10/00	9/11/2000	90	tropical depression off Cameron Parish
9/11/2000	9/12/2000	trace	
9/12/2000	9/14/2000	9	
9/22/00	9/23/00	5	
10/6/00	10/9/00	48	
11/7 & 11/8/00	11/9/00	44.5	
11/17 - 11/19/00	11/20/00	139.7	rain gauges full
11/24/00	11/27/00	32	
12/4 & 12/5/00	12/8/00	10	
12/18/00	12/19/00	51.5	
12/23 - 12/25/00	1/5/01	8	rain over Christmas weekend
1/7/01	1/8/01	10	
1/11/01	1/11/01	6	
1/16 & 1/17/01	1/18/01	34	
1/19 & 1/20/01	1/22/01	9.5	
1/29/01	2/1/01	10	
2/1/01	2/2/01	2	
2/9/01	2/12/01	4.25	
2/12 & 2/13/01	2/14/01	3	
2/28/01	3/1/01	13	
3/2/01	3/2/01	3	
3/3/01	3/5/01	94	
3/9/01	3/9/01	8	
3/12/01	3/13/01	61	
3/14/01	3/16/01	27	
3/17/01	3/20/01	18	
3/25/01	3/27/01	4.5	
3/28/01	3/30/01	53.5	
4/24/01	4/26/01	10	
5/8/01	5/9/01	8.25	

5/31/01	6/3/01	?	both rain gauges fell
6/4 & 6/5/01	6/6/01	124	tropical storm Allison
6/6 & 6/7/01	6/7/01	44	tropical storm Allison
6/7/01	6/8/01	92	tropical storm Allison
6/8/01	6/9/01	31	tropical storm Allison
6/9 & 6/10/01	6/11/01	124	tropical storm Allison
6/14/01	6/15/01	12	
6/21/01	6/22/01	64	
6/19/01	6/20/01	14	
6/26 & 6/27/01	6/28/01	16	
7/2/01	7/3/01	5	
7/4 & 7/5/01	7/5/01	33	
7/11/01	7/12/01	4	
7/13/01	7/13/01	trace	
7/21/01	7/23/01	50	
7/26/01	7/27/01	48	
7/28 & 7/29/01	7/30/01	34	
7/30/01	8/1/01	32	
8/8 - 8/13/01	8/13/01	83.5	
8/13 - 8/15/01	8/15/01	13	
8/17 & 8/18/01	8/20/01	7	
8/26/01	8/27/01	2.3	
8/28 & 8/29/01	8/29/01	40	
8/29/01	8/31/01	4.25	
9/2 - 9/4/01	9/4/01	42	
9/7 - 9/9/01	9/11/01	45	
9/19/01	9/19/01	56	
9/24/01	9/25/01	3	
10/10/01	10/11/01	2	
10/11/01	10/12/01	52	
10/13/01	10/15/01	49.5	
11/22 & 11/24	11/26/01	60	
11/29/01	11/30/01	12	
12/13, 12/14 & 12/17/01	12/17/01	26.75	
12/27 & 12/31/01	12/31/01	37	

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Matthew T. Messenger was born in 1973 on Hill Air Force Base, in Layton, Utah, to Colonel (ret.) Jay and Sherry Messenger. He moved numerous times growing up in a military family, living in Illinois, Texas, Alabama, Utah, and Virginia. He graduated from Chantilly High School in northern Virginia in 1991 and attended Mary Washington College, Fredericksburg, Virginia, for two years before transferring to Oklahoma State University to graduate with a B.S. in entomology in 1995. Then, he completed his M.S. in entomology from Kansas State University in 1998. In early 1998, he moved to New Orleans to work as a termite research entomologist for the City of New Orleans Mosquito and Termite Control Board. In New Orleans, he completed his doctoral research on the Formosan subterranean termite while maintaining a full-time position as a city employee.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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